Chapter 20
Microbe-Mediated Plant Growth Promotion: A Mechanistic Overview on Cultivable Plant Growth-Promoting Members

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Abstract The global demand for increasing agricultural productivity and declining farming land resource has posed a severe threat to crop production and agroecosystems. The use of chemical and mineral fertilizers has boosted up the agricultural productivity but considerably diminished the soil fertility, soil health, and sustainability. Improvement in agricultural sustainability requires the combined holistic approach integrating optimal use of soil fertilization, soil physical properties, soil biological processes, and soil microbial diversity, combining integrated plant nutrient management. Since past few decades, plant growth-promoting bacteria (PGPB) and plant growth-promoting rhizobacteria (PGPR) have replaced the conventional use of chemical fertilizers and pesticides in horticulture, silviculture, agriculture, environmental remediation, and cleanup strategies, and utilization of such microbial candidates for improving soil health and nutrient availability for plants is a vital practice since antiquity. Apart from the phytostimulatory effects on plants, PGPBs are potent colonizers of plant root or rhizosphere that improve both crop and soil health through various direct and indirect approaches such as nitrogen fixation, phosphate solubilization, quorum sensing, siderophore production, antimicrobials, volatile organically, mineral solubilization, induced systemic resistance, nutrient acquisition, modification of soil texture, soil porosity, etc. Increase in biomass, yield, seedling emergence, root proliferation, and timely flowering are

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the direct benefits that make these microbes most preferred in the agricultural crop production, with a high market demand. Researchers are now moving way forward to decipher their molecular mechanisms of plant beneficiation through genomic comparisons, real-time protein expressions revealing the ecophysiology, and niche adaptation that might facilitate functioning of these beneficial microbes. In this chapter, we have highlighted the status and recent trends of some important plant-beneficial bacterial members, their growth-promoting abilities, and genomic perspectives for sustainable use in crop productivity.

20.1 Introduction

Increasing agricultural productivity per unit of land and ensuring that agricultural growth responds to food security needs are the major concerns in agriculture of today. The fertilizer-based monocropping farming model that we have been following since long is not sustainable as it is harmful for human, plant, and soil health (Kumar et al. 2017a). Day by day, the food demand is increasing in the developing countries dramatically, and production of more food and fiber to feed a growing population and implementation of more efficient and sustainable production methods are challenges in today's era. In the twenty-first century, loss of productivity in the agricultural trade is due to abiotic and biotic environmental stresses (Barnabas et al. 2008). Ecological stresses are the major limiting factors for plant metabolism, growth, and productivity, especially in the arid and semiarid zones of the world. Abiotic stresses associated with soil salinity, drought, pH of soil, environmental temperature, ozone, toxic metals, and low nutrient concentration, singly or in combination, can cause lethal effects in almost all phonological stages of plant, from germination to plant enlargement limiting factors for crop production (Rengasamy 2006; Ladeiro 2012; Ashraf and Harris 2013).

Reports have been revealed the crop yield loss (70%) may be attributed to abiotic stresses, like drought. Drought is one of the major checks in agriculture (Raju et al. 2014). Drought induces changes in physiological processes of plants, together with photosynthesis, membrane integrity, enzyme stability, proline, and ABA (Karim and Rahman 2015). Bacteria, viruses, fungi, nematodes, and herbivore insect-like living organisms are the causal factors of biotic stress (Fisher et al. 2012), and they reduce agricultural yield by 30% globally. They affect the natural habitat ecology. Healthy soil conservation is a strategic element of sustainable agriculture. The noticeable solutions that can yield more agricultural products are land management, use of renewal inputs, usage of transgenic crops, and expanded practice of plant growth-promoting rhizobacteria (PGPR) (Glick 2012). PGPR is a set of soil microbial flora. They abode in the rhizosphere and on the surface of the monocot and dicot plant roots (Vacheron et al. 2013). PGPR has shown the potential to be a promising technique in the practice of supportable agriculture and could play a key role in

the mitigation of drought. The microbes colonize and impart drought by synthesizing exopolysaccharides (EPS), phytohormones, 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Govindasamy et al. 2008), volatile compounds, antioxidants, inducing accumulation of osmolytes, up- or downregulation of stress-responsive genes, and changes in root morphology at the rhizosphere/endo-rhizosphere region of the affected plant roots (Vurukonda et al. 2016). The induced systemic tolerance (IST) system, the physiological state of beneficial microbes, elicits tolerance to drought stresses (Lim and Kim 2013). Inoculation of cytokine-producing PGPR helps on growth and water stress consistence of forest container seedlings under drought condition (Liu et al. 2013). Biotic stresses even can be prevented after the use of PGPR (Gupta et al. 2015).

Based on the colonization abilities of the bacterial members, PGP microbes are broadly classified into extracellular (ePGPR) and intracellular (iPGPR) colonizers. Extracellular *PGP microbes belonging to the genera Bacillus*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Pseudomonas*, *Agrobacterium*, *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Flavobacterium*, *Micrococcus*, *Erwinia*, and *Serratia* reside in the rhizosphere or spaces between cells of the root cortex and in the rhizoplane, while intracellular (iPGPR) bacteria such as species of *Allorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Rhizobium*, endophytes, and *Frankia* are mostly associated with the root nodules (Gupta et al. 2015; Gray and Smith 2005). Accepting and enumerating the impact of PGPR on the root system and the whole plant remain challenging (Gupta et al. 2000). Studies have confirmed that PGPR are perhaps plant-specific genotype and cultivar (Bashan 1998; Lucy et al. 2004). The molecular mechanisms of PGPR affect the architecture of the root system and interfere with the plant hormonal pathways (Vacheron et al. 2013). The two-way cross talk between microbes and plant host for plant growth promotion is presented in Fig. 20.1.

20.2 Mechanisms of Plant Growth Promotion

The mechanisms of plant growth differ between species and strains; so, typically, not a single mechanism is accountable for plant growth promotion. PGPR enhances plant growth either by following direct or indirect mechanisms (Glick 1995; Gupta et al. 2000; Kumar et al. 2012, 2016a) or a combination of both (Fig. 20.2) corresponding to siderophore production, biological nitrogen fixation, phosphate solubilization (Richardson et al. 2009; Ortiz Castro et al. 2009; Hayat et al. 2010; Kumar et al. 2017b), rhizosphere engineering, production of 1-aminocyclopropane-1-carboxylate deaminase (ACC), quorum sensing (QS) signal interference and inhibition of biofilm formation, phytohormone production, antimicrobial activity (Yuwono et al. 2005), and volatile organic compound (VOC) production (Bhattacharyya and Jha 2012). Direct mechanisms, facilitating resource acquisition and modulating phytohormone levels, affect the plant's metabolism and balance plant growth regulators by leading to an increase in its adaptive capacity and

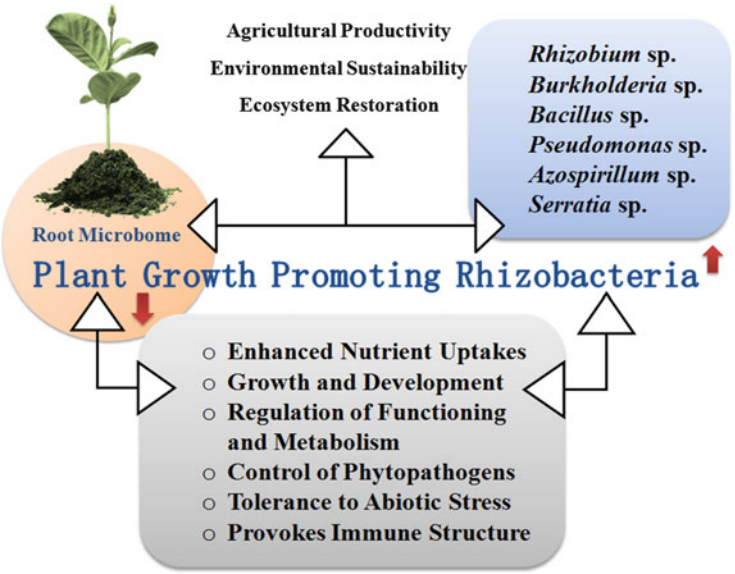

Fig. 20.1 Multifaceted diagram of bidirectional response of PGPR and host for plant growth promotion

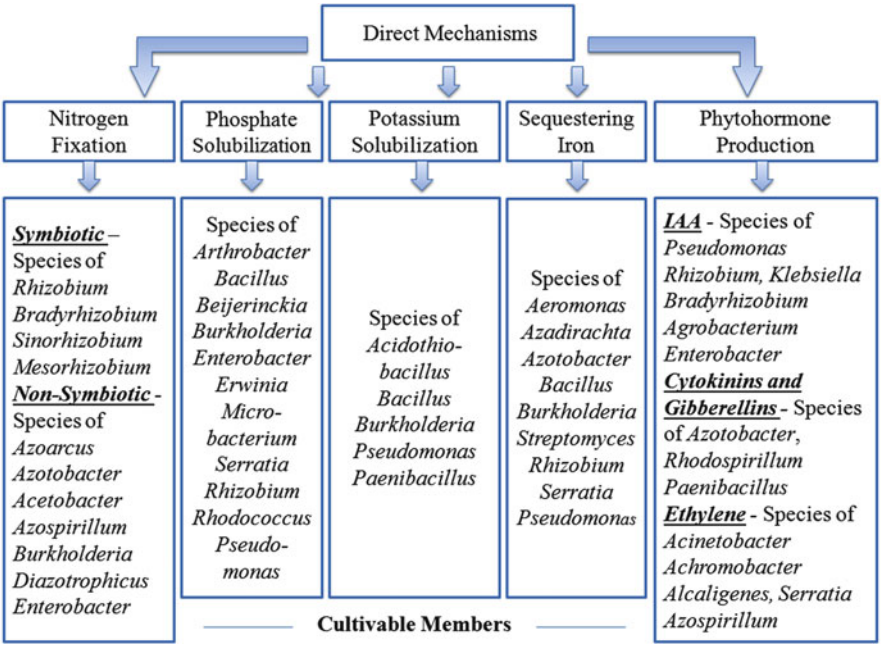

Fig. 20.2 Direct plant growth promotion by bacteria

releasing hormones. Plants and colonization of bacteria have cohabited for millions of years. They live and promote the healthy growth of plant. Facilitating resource acquisition is categorized as nitrogen fixation, potassium solubilization, iron sequestering, and phosphate solubilization (Glick 2012).

20.2.1 Nitrogen Fixation

Nitrogen, being the vital nutrient required for plant growth, and nitrogenase (*nif*) are the key players in providing available N (NH_4^+) to the plant through biological nitrogen fixation. Nitrogenase includes structural genes that are involved in the initiation of the Fe protein, biosynthesis of the molybdenum cofactor, and electron donation and regulatory genes for the synthesis and function of the enzyme. The most critical fixation gene, *Nif*, is typically present in a cluster of around 20–24 kb with 07 operons encoding 20 different proteins (Ahemad and Kibret 2014). Nitrogen-fixing microbes are generally categorized as (a) symbiotic N_2-fixing bacteria like species of *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium*, *Azoarcus*, *Azotobacter* and (b) nonsymbiotic N_2-fixing bacteria, viz., species of *Azospirillum*, *Diazotrophicus*, *Gluconacetobacter*, *Burkholderia*, *Acetobacter*, and *Enterobacter* (Kumar et al. 2013a; Kumar 2017).

20.2.2 Phosphate and Potassium Solubilization

The phosphate solubilization mechanisms include the release of complexing or mineral-dissolving substances such as organic acid protons, anions, CO_2, hydroxyl ions, and siderophores, the liberation of extracellular enzymes, and the emancipation substrate degradation (McGill and Cole 1981; Sahoo et al. 2017). Species of *Bacillus*, *Burkholderia*, *Microbacterium*, *Rhizobium*, *Enterobacter*, *Rhodococcus*, *Beijerinckia*, *Arthrobacter*, *Serratia*, *Erwinia*, *Flavobacterium*, and *Pseudomonas* are documented as phosphate solubilizers. Members of *Pseudomonas*, *Paenibacillus*, *Burkholderia*, *Acidithiobacillus ferrooxidans*, *Bacillus edaphicus*, and *Bacillus mucilaginosus* (Goswami et al. 2016) are standard potassium (K) solubilizers. These bacterial groups convert insoluble form of K in the soil to soluble forms, through various chemical reactions like exchange reactions, chelation, and acidification (Masood and Bano 2016).

20.2.3 Sequestering Iron (Siderophore)

Iron is an essential element and plays a key role in various physiological processes like DNA synthesis, respiration, and photosynthesis along with key factors of

many enzymes and Fe–S cluster (Dellagi et al. 2009), but the availability of soluble Fe is limited because of its low solubility at neutral pH. Microorganisms secrete high-affinity iron-chelating compounds in low Fe environments which refer to siderophores as the strong iron-chelating agents. These are water-soluble, and extracellular and intracellular siderophores, which have greater affinity for Fe, are synthesized by almost all microbes under iron limitations. Siderophores produced by the same genus are homologous, while others that could utilize those produced by other rhizobacteria of various genera are heterologous siderophores. Loper and Buyer (1991) reported the production of siderophore by different bacterial genera, like pyoverdines by *Pseudomonas* spp., hydroxamates by *Erwinia carotovora* and *Enterobacter cloacae*, catechols by *Agrobacterium tumefaciens* and *Erwinia chrysanthemi*, and rhizobactin by *Rhizobium meliloti*. Species of *Aeromonas*, *Streptomyces*, *Rhizobium*, *Bacillus*, *Azadirachta*, *Burkholderia*, *Serratia*, *Azotobacter*, and *Pseudomonas* are grouped as iron-chelating bacteria. In these rhizobacteria, Fe^{3+} siderophore complex is reduced to Fe^{2+} which is further released into the cell from the siderophore via the inner and outer membrane linking (Parker et al. 2007). The siderophores are destroyed/recycled during the process. The microorganisms producing siderophores have also a major role in the disease suppression of soil-borne disease especially toward fusarium wilts by the action of siderophore-mediated iron competition as well as inducing systemic resistance in plants (Leeman et al. 1996; Meziane et al. 2005).

20.2.4 Modulating Phytohormone Levels

Plant growth-regulating hormones are called phytohormones, namely indole acetic acid (IAA), ethylene, cytokinins, and gibberellins (Glick 2012; Kumar et al. 2013b; Kumar and Mishra 2014). Auxin production is mediated by tryptophan (Trp)-dependent and *Trp*-independent pathways (Wani et al. 2016). Several beneficial effects have been documented for indole acetic acid, viz., regulation in plant cell division and differentiation; stimulatory effects on germination of seed and tuber; development of root and xylem; management of vegetative growth; formation of lateral and adventitious root; effective response to light, gravity, and fluorescence; affects photosynthesis; pigment formation; biosynthesis of various metabolites; and resistance to biotic/abiotic stresses (Glick 2012).

Members of the genera *Pseudomonas*, *Rhizobium*, *Bradyrhizobium*, *Agrobacterium*, *Enterobacter*, and *Klebsiella* are good at IAA production. Ethylene, a gaseous phytohormone, is biosynthesized from methionine via S-adenosyl-L-methionine (AdoMet) and the cyclic nonprotein amino acid ACC (Wani et al. 2016). ACC synthase converts AdoMet to ACC, while ACC oxidase catalyzes the conversion of ACC to ethylene. Species of *Acinetobacter*, *Achromobacter*, *Alcaligenes*, *Azospirillum*, *Ralstonia*, and *Serratia* are ethylene producers. Ethylene also plays a key role in the defense to heat stress. The cytokinins are master regulators during plant growth and development. They increase their endogenous levels via uptake

and enhanced biosynthesis. The gibberellins are tetracyclic diterpenoid carboxylic acids, and few of them function as growth hormones in higher plants, of which GA1 and GA4 are the predominant ones. They are effective counters to seed germination, leaf expansion, stem elongation, flower and trichome initiation, and flower and fruit development. Members of the genera *Azotobacter*, *Pantoea*, *Rhodospirillum*, and *Paenibacillus* are effective cytokinin and gibberellin producers.

20.2.5 Induced Systemic Resistance

The ability of the plant to resist against the disease and develop a defense to overcome it is known as induced systemic resistance (ISR). ISR is directly linked to physiological tolerance with microbial antagonisms in the rhizosphere region as well as production of phytoalexins as a consequence of defense response. Metabolism of jasmonic acid is the major key player in the whole process. PGPR produce antagonistic substances like siderophores, antibiotics (Mageshwaran et al. 2010, 2012), antimicrobial peptides, acyl homoserine lactones, and volatile compounds (acetoin and 2,3-butanediol) that help plant resist against microbial pathogens, thus enhancing plant growth promotion (Weller et al. 2002). Several strains of *Pseudomonas* sp., *Pseudomonas syringae*, and *Pseudomonas stutzeri* have been applied effectively against phytopathogens like *Colletotrichum* and Fusarium wilt diseases (El-Badry et al. 2006). Application of several *Bacillus* species (*B. amyloliquefaciens*, *B. mycoides*, *B. sphaericus*, and *B. subtilis*) is reported to cause significant reduction in disease incidence (Ryu et al. 2004; Govindasamy et al. 2010) in varied field condition experiments. Productions of defense-related enzymes like peroxidase, polyphenol oxidase, β-1,3-glucanase, chitinases, and phenylalanine are the most primary mechanisms of PGPR for inducing SR against *Fusarium oxysporum* and *Rhizoctonia solani* (Dutta et al. 2008). There are reports describing many potential *Pseudomonas* strains (AN-1-UHF, AN-5-UHF, PN-7-UHF, and PN-13-UHF) to produce proteolytic enzymes which have a very pivotal role in plant growth promotion of apple and pear (Ruchi et al. 2008). Combinations of such strains with other biocontrol agents pose a potent synergistic inhibitory effect against pathogens and in the promotion of plant growth.

20.2.6 Volatile Organic Compound Production

Some specific PGPR strains are found to release some mixed chemicals also known as volatile organic compounds (VOCs) which have a noteworthy role in plant growth promotion. These volatile compounds have also an important role in the mechanism for the stimulation of growth of plants by rhizobacteria. These compounds have also a major task in ISR mechanisms (Ryu et al. 2004). Some major volatile compounds mostly produced by PGP microbes belong to the class of

acetaldehyde, ethanol, hydroxyurea, cycloserine, butanal, ethoxyethene, 2-butanol, 1-butanol, 2-methyl,1-propanol, 2-pentanone, 3-hydroxy-2-butanone, 2-ethyl-1-butanol, methoxy-phenyl-oxime, benzaldehyde, dimethyl disulfide, 2-heptanone, dimethyl trisulfide, trimethyl pyrazine, 2-ethyl 1-hexanol, 2-phenyl ethanol, phenyl acetaldehyde, etc. There are some volatile organic compounds, viz., 2,3-butanediol and acetoin, which have been found to be released by certain PGPR strains like *Bacillus subtilis* GB03, *Bacillus amyloliquefaciens* IN937a, and *Enterobacter cloacae* JM22 that have a major role in plant growth promotion of *Arabidopsis thaliana* (Ryu et al. 2003). In *Arabidopsis* against *Erwinia carotovora*, the compounds secreted by these *Bacillus* species have also been able to induce ISR (Ryan et al. 2009). VOCs produced by the rhizobacterial strains can act as signaling molecules in the mediation of plant–microbe interactions as volatiles produced by PGPR colonizing roots are generated at adequate dose to activate the plant responses (Ryu et al. 2003). Some plant volatiles having low molecular weight, viz., jasmonates, terpenes, and green leaf components, as effective signal molecules for living organisms in different trophic levels have also been recognized (Farmer 2001) which have several roles in plant defense mechanisms.

20.2.7 Indirect Mechanisms

Plant growth-promoting microbes indirectly and effectively enhance the plant defense strategies against phytopathogens through several ways (Fig. 20.3), and these processes happen outside the plant, with the involvement of the plants' defensive developments (Goswami et al. 2016). The defensive setups are maintained by the presence of the species of *Bacillus*, *Streptomyces*, *Pseudomonas fluorescens*, *Pseudomonas putida* and *Stenotrophomonas*, *Bradyrhizobium*, *Rhizobium*, *Serratia*, and *Streptomyces.* Productions of antibiotics (streptomycin, oligomycin A, butyrolactones, oomycin A, kanosamine, phenazine-1-carboxylic acid, pyrrolnitrin, pyoluteorin, xanthobaccin, viscosinamide, zwittermicin A, and 2,4-diacetylphloroglucinol) prevent the growth of plant pathogens in the vicinity of the plant root (Whipps 2001; Govindasamy et al. 2010; Kumar et al. 2016b), having a broad-spectrum activity. These antibiotics are effective against many phytopathogenic fungi belonging to *Basidiomycetes*, *Deuteromycetes,* and *Ascomycetes*, including *Botrytis cinerea*, *Rhizoctonia solani*, *Sclerotinia sclerotiorum* (Kumar et al. 2016b), and *Verticillium dahliae* (Raaijmakers et al. 2010).

Secretion of microbial extracellular lytic enzymes including chitinases, cellulases, β-1,3-glucanases, proteases, and lipases can lyse a portion of the cell walls of many pathogenic fungi of *Fusarium* and *Rhizoctonia* member groups. Production of laminarinase and extracellular chitinase is produced by *P. stutzeri* lyse mycelia of *F. solani*. *Pseudomonas* strains, AN-1-UHF, AN-5-UHF, PN-7-UHF, and PN-13-UHF, were reported to produce lytic enzymes especially proteolytic enzymes which have a significant role in the plant growth promotion of apple and pear (Ruchi et al. 2008). *Bacillus* species isolated from different tomato rhizospheric soil are also

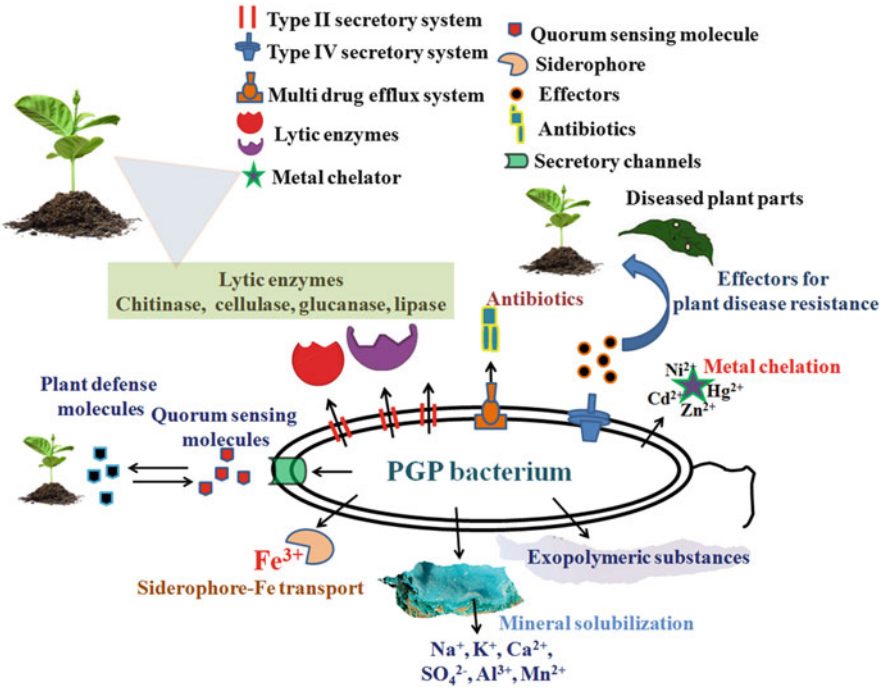

Fig. 20.3 Multifaceted diagram of indirect mechanisms of plant growth promotion by PGP microbe

found to secrete several hydrolytic enzymes such as β-1,3-glucanase, protease, chitinase, and cellulose which have a vital role in plant growth promotion and plant disease management (Kumar et al. 2012). Chitinolytic *Pseudomonas* isolate has also showed a pronounced antifungal activity (Velazhahan et al. 1999). PGP bacteria induce defense systems by inducing systemic acquired resistance and induced systemic resistance (López-Bucio et al. 2007).

The resistance mechanisms reduce the phytotoxic microbial communities and also elicit induced systemic tolerance to abiotic stress (Yang et al. 2009). Solubilization of minerals by PGP microbes (highly specialized lithoautotrophs) is one of the most interesting feature for the availability of inorganic nutrients like K, Na, Ca, and other trace elements by producing inorganic acids (HNO_3, H_2SO_4) as an end product of their metabolism. Members belonging to the genus *Thiobacillus* (S metabolizing) and nitrifiers (*Nitrosomonas* and *Nitrobacter*) are the prominent bacterial members solubilizing rock minerals (K/Ca bearing or PO_4^{3-} minerals). Thiobacilli members (*T. thiooxidans*, *T. ferrooxidans*) are acidophilic or acid tolerant (below pH 1–2), are able to fix CO_2, and use reduced inorganic S compounds. Nitrifying bacteria use urea, ammonium compounds, nitrite, and NO as energy source and some organic compounds for the production of acid on mineral surfaces (concrete, natural stone, glass, feldspar minerals). Some microbial members are potent producers of CO_2 as

the major end product, where CaO, $Ca(OH)_2$, and $CaSiO_2$ react with CO_2 to form $CaCO_3$ in the process of carbonatization, resulting in the decrease of pH from 12.5 to around 8.5 and the subsequent iron/concrete corrosion. The organic acids produced by microbes are having two modes of action of minerals: (a) action of protons and (b) chelation of metal ions. Acids like acetic, gluconic, glucuronic, oxalic, oxaloacetic, succinic, malic, glyoxylic, and others are the most favorable for solubilization processes.

Along with these, other organic acids (amino acids) and polysaccharides are also excreted outside by the microbial cells as a result of unbalanced growth, metabolic bottlenecks, surplus of substrates, or limited supply of nutrients (P, N, K, etc.). Production of organic acids (acetic, butyric, formic, fumaric) and organic solvents (ethanol, butanol, propanol, lactate, acetoin, aldehydes, etc.) as a result of fermentation is also the potential contributor for partial dissolution, swelling, and wear-tear of minerals. Some plant growth-promoting microbes produce exopolymeric substances containing sugars, sugar acids, and amino acids that act as complexing agents and also as metal chelators facilitating reduced metal stress in root rhizosphere. Microbial action of the production of biotic elicitors is also promising in developing defense system of plants, where chemical stimuli activate the production of phytoalexin-type molecules, which elicit morphological and physiological responses in plants in opposition to phytopathogens (Sekar and Kandavel 2010). Compounds like serpentine, ajmalicine, crocetin, picrocrocin, scopolamine, hyoscyamine, and tanshinone are the major stimulatory chemicals produced by PGP microbes for plant defense against pathogenic organisms.

20.3 Taxonomy of Candidate PGP Microbes

Taxonomy, systematics, biosystematics, scientific classification, biological classification, and phylogenetics have allied meanings in records. Classification of small and simple shapes holding bacteria on the basis of morphological characterization is extremely difficult. Besides shape, bacteria are well identified and classified on the basis of their biochemistry and growth conditions. They take account of media, morphology, antibiotic sensitivity, biochemical tests, serological methods, and bacteriophage typing, together constituting the chemotaxonomic and physiological characterization. Recent developments in taxonomic studies including genotypic characters (G+C % content, DNA–DNA homology % based on HPLC and TM methods, whole genome-based average nucleotide identity, average amino acid identity, tetra correlation among nucleotides, pulse-field gel electrophoresis), chemotaxonomic characters (fatty acid methyl esters, cell wall polyamines, cellular sugars, polar lipids, respiratory quinones, cellular amines), characters (pigments, colony properties), numerical taxonomy (computer-assisted characterization like correlation based on Jaccard's coefficient, simple matching coefficient, Spearman coefficient), and genomic (multilocus sequence typing, pan genomics ribosomal protein sequences, genome relatedness from whole genome) have revolutionized

the characterization of many species. The details of the taxonomic markers and their resolution in bacterial systematics are presented in Fig. 20.4. Current strategies of integrating multiple omics technologies like whole genome sequencing (functional and comparative genomics), proteomics (whole-cell and membrane associated), transcriptomics (total RNA pool sequencing), along with matrix-assisted laser desorption ionization-time-of-flight mass spectrometry (MALDI-TOF-MS) have shown high potentiality in evolutionary biology to consider how differently bacteria are associated and evolved (Jia et al. 2015) and their complete physiological as well as genetic cataloging.

20.4 Genus *Rhizobium:* Associative Symbiotic and Free-Living N_2 Fixers

The genera *Azorhizobium*, *Bradyrhizobium*, *Burkholderia*, *Devosia*, *Ensifer*, *Methylobacterium*, *Mesorhizobium*, *Microvirga*, *Ochrobactrum*, *Phyllobacterium*, *Rhizobium*, *Shinella* of *Alphaproteobacteria*, and *Cupriavidus* of *Betaproteobacteria* and some *Gammaproteobacteria* form the set of rhizobia (Berrada and Fikri-

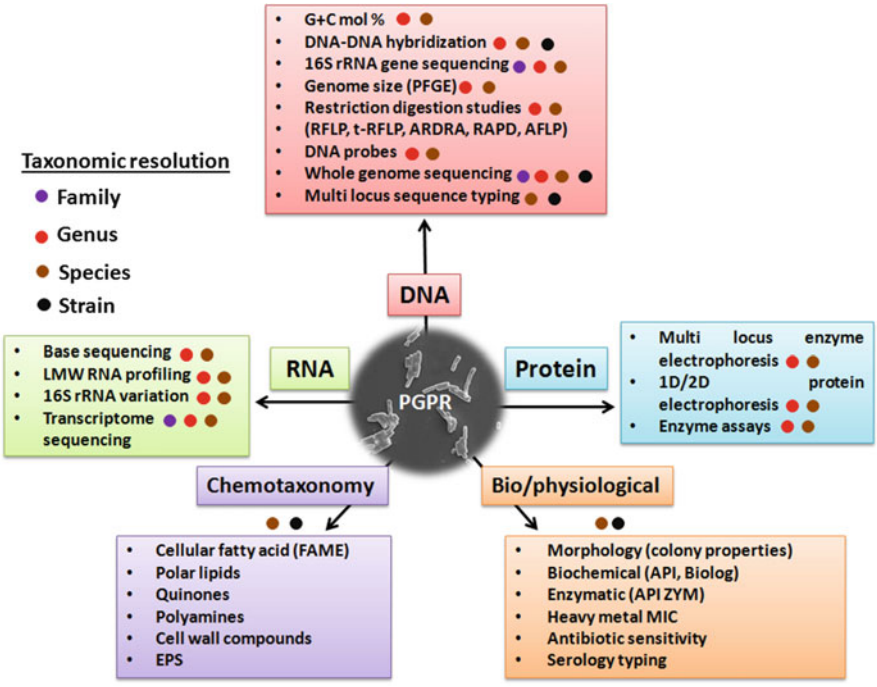

Fig. 20.4 Schematic overview of taxonomic methods used for characterization of microbial candidates and their resolution

Benbrahim 2014). Among all, the members of the genus *Rhizobium* are the most studied for its N_2 fixation ability and supportive plant growth-promoting behavior. Members are Gram-negative, aerobic to facultative anaerobic, nonsporulating, motile rods of 0.5–0.9 × 1.2–3.0 μm (Zakhia and de Lajudie 2001; Willems 2006), mostly attributed to symbiotic N_2 fixation as well as free-living forms (Mohapatra et al. 2016). Since its first description by Frank (1889), 94 validly named species (LPSN, http://www.bacterio.net/) were affiliated to the genus *Rhizobium*. G+C % is on average 59–64 mol%. Colonies are found circular, semitranslucent, raised, and 2–4 mm in diameter within few days of inoculation on solid medium. Turbidity develops in liquid medium after 2 or 3 days. They are chemoorganotrophic in nature. Optimum pH and temperature range between 6–7 and 25–30 °C, respectively. *Rhizobium* is often located in the nodules of beans, peas, and groundnuts. Strains seem host specific in many cases. The bacterial colonization is able to invade the root hairs naturally. In nodules, bacterial clusters fix atmospheric nitrogen into ammonia for plants (Frank 1889). Study shows *Rhizobium* resists chloramphenicol, polymyxin B, erythromycin, neomycin, and penicillin (Cole and Elkan 1979).

On the basis of scientific classification, *Rhizobium* comes under kingdom, *Bacteria*; phylum, *Proteobacteria*; class, *Alphaproteobacteria*; order, *Rhizobiales*; and family, *Rhizobiaceae*. For cultivation and isolation of *Rhizobium* species, yeast mannitol agar and *Rhizobium* medium are used (Gulati 1979). Yeast extract, mannitol, dipotassium phosphate, magnesium sulfate, sodium chloride, and agar are the key components of the medium. *Rhizobium* genus includes *R. galegae* (Mousavi et al. 2014) isolated from the nodules of wild *Galega orientalis* and *Galega officinalis*; *R. gallicum* (Amarger et al. 1997) cultivated in Europe and Tunisia from flat-podded variety of nodulating beans, i.e., *Phaseolus vulgaris*; *R. indigoferae* (Wei et al. 2002) isolated from Indigo fera shrubs; *R. leguminosarum* (Frank 1889; Noel et al. 1996) isolated from canola and lettuce; *R. loessense* (Wei et al. 2003) isolated from nodules of *Astragalus* and *Lespedeza* species; *R. lusitanum* (Valverde et al. 2006) isolated from *Phaseolus vulgaris* and *Leucaena leucocephala*; *R. mongolense* (van Berkum et al. 1996) isolated from Inner Mongolian *Medicago ruthenica*; *R. bangladeshense*; and *R. binae* (Rashid et al. 2015) isolated from root nodules of lentils in Bangladesh. The members are well distributed in soil with immense ecological as well as agricultural significance for their ability to fix nitrogen (N_2) in legume crops for their ability to form root nodules on legumes and fix N_2 (Viteri and Schmidt 1987; Young et al. 2001), with 94 species being in standing nomenclature (http://www.bacterio.net/rhizobium.html). In recent years, new members have been isolated from diverse nonlegume niches including sand dunes, effluent treatment plant, activated sludge, bioreactor, pesticide-contaminated sites, freshwater river, and sea water. New members are also described to degrade various pollutants, heavy metals, and hydrocarbons like naphthalene (*R. naphthalenivorans*; Kaiya et al. 2012), selenite reduction (*R. selenitireducens*; Hunter et al. 2007), exopolysaccharide production (*R. alamii*; Berge et al. 2009), aniline (*R. borbori*; Zhang et al. 2011), use of PAH (*R. petrolearium*; Zhang et al. 2012), and triazophos (*R. flavum*; Gu et al. 2014).

20.5 Genus *Pseudomonas:* Plant Beneficial, Pollutant Degrader

In 1894, the *Pseudomonas* group was depicted as the most assorted and ever-present bacterial genera like Antarctica to the tropics and described to include Gram-negative, strictly aerobic rods that are motile by polar flagella (Skerman et al. 1980). *Pseudomonas* species have been cultured from all kinds of environments worldwide, in sediments, water, soil, the sea, deserts, the plant rhizosphere, fungi, diseased animal specimens, and human clinical samples. *Pseudomonas* strains can linger their constancy in diverse habitats and under very unpleasant circumstances. Over decades, the taxonomy of the *Pseudomonas* genus has been controversial for other bacterial taxa (Peix et al. 2009). Based on the 16S-rRNA similarity, currently there are 140 species belonging to the genus *Pseudomonas* which are termed as *sensu stricto* group I with names that have standing in nomenclature in LPSN (http://www.bacterio.net/pseudomonas.html).

The members are aerobic, Gram-negative, straight or slightly curved rods, 0.5–1.0 μm in diameter, and 1.5–5.0 μm in length. *Pseudomonas* are motile with one or several polar flagella. Some species are found well particular in forming poly-β-hydroxybutyrate as the carbon-storage granule, which appears as sudanophilic inclusions. No resting stages are documented. *Pseudomonas* is not fussy in general. They can grow up on protein hydrolysate, magnesium chloride, and potassium sulfate kind intermediates containing agar media. Species-specific *Pseudomonas* isolation agars also contain cetrimide, nalidixic acid, cephaloridine, penicillin G, pimaricin, malachite green, and glycerol. According to biochemical characterization, *Pseudomonas* shows catalase positive, Voges–Proskauer, and indole and methyl red negative in general. An additional attribute associated with *Pseudomonas* species is that they ooze a yellowish green fluorescence, called pyoverdine, pyocyanin as a blue pigment, a reddish pigment called pyorubin, and pyomelanin as brown function under iron-limiting conditions, as a siderophore, but few secrete quinolobactin as yellow/dark green in the presence of iron. *Pseudomonas* strains are reported to produce IAA, HCN, siderophores, phenazines, cyclic lipopeptides, pyoverdine, and quorum-sensing signaling compounds (Gupta et al. 2014; Kumar et al. 2016b). On the other hand, *Pseudomonas* strains have been executed using MALDI-TOF-MS for excellent identification results (Pineda et al. 2010).

According to the scientific classification, *Pseudomonas* comes under kingdom, *Bacteria*; phylum, *Proteobacteria*; class, *Gammaproteobacteria*; order, *Pseudomonadales*; family, *Pseudomonadaceae*; genus, *Pseudomonas*; and species, *P. fluorescens*, *P. aurantiaca*, and *P. putida. Pseudomonas fluorescens* strains play a major role in plant growth promotion, induction of systemic resistance, and action as bacterial antagonist to control pathogenic bacteria and fungi. It is a potential biopesticide for augmentative biological control of several diseases and bioremediation of various unrefined compounds in agriculture and horticulture (Ganeshan and Kumar 2005). *Pseudomonas aurantiaca s*trains are generally orange-colored soil bacterial members. Rhizosphere soils of sugarcane, soya bean, canola, and potatoes

are the customary habitats of such species. The bacterium produces di-2,4-diacetylfluoroglucylmethan. Di-2,4-diacetylfluoroglucylmethan is a natural phenol compound, which inhibits the growth of phytopathogens and promotes plant growth indirectly. Based on 16S rRNA analysis, *Pseudomonas aurantiaca* is a subspecies of *Pseudomonas chlororaphis* (Peix et al. 2007). *Pseudomonas putida* strains harbor multi-plasmid hydrocarbon-degrading genes (called degradative plasmids). They are the first patented organisms in the world. *P. putida* has been confirmed as a potential biocontrol agent with effectual antagonist activity on damping off diseases such as *Pythium* (Amer and Utkhede 2000) and *Fusarium* (Validov et al. 2007).

20.6 Genus *Bacillus*: Dominant Cum Abundant Members

The majority of *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Bacillus amyloliquefaciens*, *Bacillus subtilis*, *Bacillus cereus*, *Bacillus megaterium*, *Bacillus lipopeptides*, *Bacillus pasteurii*, *Bacillus pumilus*, *Bacillus mycoides*, and *Bacillus sphaericus* are distributed globally with the extensive amount of ability to promote plant growth and have been widely recognized (Govindasamy et al. 2010). The growth promotion includes production of siderophore, phytohormones and antibiotics, solubilization and mobilization of phosphate, inhibition of plant ethylene production, and induction of efficient pathogen resistance (Whipps 2001; Gutiérrez-Mañero et al. 2001; Idris et al. 2007; Richardson et al. 2009). Multilayered chambers of cell wall, secretion of peptide signal molecules and peptide antibiotics, with extracellular enzymes, contribute to survival under unfavorable conservation for extensive periods of time. Repressing capability of plant pathogens by *Bacillus subtilis* and *Bacillus cereus* has been widely recognized. Genus *Bacillus* was named in 1835 by Christian Ehrenberg. By Ferdinand Cohn, *Bacillus* was further characterized as most ubiquitous, spore-forming, Gram-positive, aerobic/facultative anaerobic bacteria. *Bacillus* has expanded to extreme phenotypic variety and heterogeneity. Today, *Bacillus* holds 243 types of species with cultivable isolates (16S rRNA gene sequences >1200 bp) from varied environments (https://rdp.cme.msu.edu/hierarchy/hierarchy_browser/Bacillus), where only 19 types of strains have been reported to be from plants or plant-associated niches.

20.7 Genus *Azotobacter:* Free-Living N_2 Fixers

Azotobacter is a motile, free-living aerobic bacterium with a genomic content of G−C of 63–67.5% (T_m) (Becking 1981). This heterotrophic group of bacteria has thick-walled cysts which may produce large quantities of capsular slime. The particular genus plays an important role in nitrogen cycle as nonsymbiotic nitrogen fixer and acts as PGPR. The bacterial group makes possible the root expansion, improves nutrient uptake potentiality, protects from plant diseases, and increases

biomass production in the rhizosphere region of nearly every one of the crops (Kasa et al. 2015). They are distributed in soils, water, and sediments. *Azotobacter chroococcum*, an oval or a spherical kind of Gram-negative bacterium, was revealed and explained by Martinus Beijerinck in 1901 for the first time (Beijerinck 1901; Mrkovacki and Milic 2001). Lipman stated about *Azotobacter vinelandii* in 1909 and in 1904 on the subject of *Azotobacter beijerinckii*, which he named in the admiration of Beijerinck. In 1949, Russian microbiologist Nikolai Krasilnikov identified the species of *Azotobacter nigricans. Azotobacter nigricans* was divided into two subspecies—*Azotobacter nigricans* subsp. *nigricans* and *Azotobacter nigricans* subsp. *achromogenes* in 1981 by Thompson Skerman. Again, in the year 1981, Thompson and Skerman described *Azotobacter armeniacus.*

In 1991, Page and Shiv Prasad informed concerning *Azotobacter salinestris*—a micro-aerophilic and air-tolerant bacterium. According to the taxonomical division, *Azotobacter* comes near the domain, *Bacteria*; phylum, *Proteobacteri*a; class, *Gammaproteobacteria*; order, *Pseudomonadales*; and family, *Pseudomonadaceae/Azotobacteraceae* (Becking 1999), with most members reported to be described as *A. vinelandii* or *A. chroococcum.* Morphological similarity and biochemical uncertainty with FNFB like *Derxia*, *Azomonas*, and *Beijerinckia* are the difficulties in characterizing *Azotobacter* species. In 2004, a phylogenetic study has shown that *Azotobacter vinelandii* evolved from *Pseudomonas aeruginosa*. After years, in 2007, the genera *Azotobacter*, *Azomonas*, and *Pseudomonas* were publicized as allied or might be synonyms.

20.8 Genomic Insight and Behavior of Some Plant Growth-Promoting Microbes

Of today, 20,584 eubacterial and 907 archaebacterial candidates have been described, out of which 9966 non-type bacterial, 3890 type bacterial, and 210 archaebacterial genomes have been sequenced. The use of genome sequencing through next-generation sequencing (NGS) approach with massively parallel sequencing capacity, high depth coverage, and cost-effective features has moved the basics of bacterial species designation, taxonomy, and phylogeny to a next level termed as "taxonogenomics or phylogenomics." Complete genome projects are enabling the researchers to study the genetic and functional relatedness between organisms at the whole-cell level, thus far beyond conventional 16S rRNA-based phylogeny system. Genetic events such as horizontal gene transfer (HGT), gene rearrangements, plasmid functions in species evolution, and niche adaptation, have become a newer attraction for the geneticists with the high affordability and accessibility to general microbiology laboratories. Completed genome projects with genome features of some candidate PGPR strains are presented in Table 20.1. Recently, NGS has been used to study genomes of different PGPR (free-living and endophytic strains) mainly isolated from crop species such as rice, maize, wheat,

potato, sugarcane, barley, coffee, tea, soybean, etc. and are presented in Table 20.2, with their plant-beneficial properties.

The microbiology of the rhizosphere has been thoroughly studied for more than 100 years, but study on endosphere and the organisms associated (endophytes) remains largely unexplored. Endophytic microbes reside within various tissues of the host plant in a commensal or beneficial manner, and endophytic microbiome is known for its antagonistic activity against pathogens (Berg et al. 2013). They are found to be the promising source of natural metabolites with potential benefits to plant as well as other animals because of their significant bioactivities and medical importance (Kaul et al. 2012; Premjanu and Jayanthy 2012; Mousa and Raizada 2013; Kusari et al. 2014). Endophytes are also beneficial for the host plants with biotic and abiotic stress tolerance, nutrient acquisition, and plant growth promotion (Rodriguez et al. 2008; Kumar et al. 2013c). Genome sequencing has revealed the genetic inventory of these organisms with capability for various plant growth-promoting properties like nitrogen fixation, production of phytohormone (IAA, GA, etc.), mineral acquisition (Fe, P, K), biotic/abiotic stress tolerance, and other nutrient cycling processes (Fouts et al. 2008; Firrincieli et al. 2015; Martinez-Garcia et al. 2015). Recent studies have provided greater understanding on the mode of endophytism in plant root and other plant hosts through gene coding for *N*-acyl homoserine lactone synthases, hydrolases, adherence factors, and fusaric acid resistance in *Pantoea ananatis* (Megias et al. 2016). Genomes of such entophytes (*Gluconacetobacter diazotrophicus* Pal5, *Stenotrophomonas maltophilia* R551-3, *Pseudomonas fluorescens* PICF7, *Kosakonia oryzae* K0348, *Raoultella terrigena* R1Gly, *Bacillus thuringiensis* KB1, *Pseudomonas putida* W619, *Azospirillum* sp. B510, *Variovorax paradoxus*, *Herbaspirillum seropedicae* strain SmR1, *Burkholderia phytofirmans* strain PsJN, *Burkholderia* sp. strain KJ006, *Pseudomonas poae* RE*1-1-14, *Paenibacillus* sp. P22, *Pantoea agglomerans*, *Pseudomonas* sp. strain RIT288, *Janthinobacterium lividum*) are served to be the model systems for studying entophytic plant–microbe interactions. The concept of PGPR-mediated plant growth promotion is gaining worldwide importance and acceptance and has been applied on a wide range of crops including cereals, pulses, vegetables, oilseeds, and plantation crops. Combination of the use of these microbes in plant disease management and the solutions of soil nutrient management might provide ample advantages to agriculture.

20.9 Conclusions and Future Prospects

To avert the lack of sufficient amount of one or more nutrient sources such as nitrogen, iron, and phosphorus and also to obtain higher crop yields, it would obviously be advantageous if efficient biological resources of providing nitrogen, iron, and phosphorus to plants could be commercialized to substitute inexpensive chemical nitrogen, iron, and phosphorus that are currently used. Plant growth-promoting bacteria (PGPB) modulates plant stress indicators under environmental

Table 20.1 Genomic properties of PGPR bacteria as obtained through whole genome sequencing from JGI-IMG database

Genomes	GOLD ID	Size (/10)	Genes	GC	CDS	RNAs	rRNA	tRNAs	COGs	KOG	Pfams	Enzymes	SP	TMH	HTG
R. populi CCTCC AB 2013068	Gs0129175	52.73	5118	0.7	5052	66	3	47	3861	919	4405	1287	399	1170	370
R. leguminosarum bv. trifolii WSM1325	Gs0011842	74.18	7292	0.6	7232	60	9	51	5011	1279	5945	1641	652	1633	132
R. subbaraonis DSM 24765	Gs0129175	65.82	6367	0.6	6289	78	4	48	4332	1024	5084	1412	524	1450	241
R. miluonense HAMBI 2971	Gs0110196	68.08	6493	0.6	6426	67	5	47	4883	1221	5567	1591	557	1510	83
R. rhizosphaerae MH17	Gs0135582	55.34	4924	0.7	4852	72	3	53	3618	874	4077	1235	377	1139	25
R. flavum CCTCC AB 2013042	Gs0129175	46.42	4596	0.6	4528	68	3	47	3346	860	3846	1179	428	1118	45
R. etli 8C-3	Gs0128632	73.09	7131	0.6	7030	101	10	57	4902	1185	5719	1573	586	1582	52
R. giardinii bv. giardinii H152	Gs0014878	68.10	6691	0.6	6618	73	2	48	4585	1171	5471	1668	556	1491	101
R. leguminosarum bv. phaseoli 4292	Gs0014878	73.47	7193	0.6	7109	84	9	53	5163	1289	5983	1677	622	1615	10
R. leguminosarum bv. Trifolii	Gs0000556	72.06	6766	0.6	6755	79	3	68	5122	1227	4988	1433	654	1025	35
R. yantingense CCTCC AB 2014007	Gs0129175	58.16	5580	0.6	5507	73	3	51	4098	950	4621	1313	498	1348	85
R. acidisoli FH23	Gs0117713	73.44	7111	0.6	7028	83	3	53	4948	1234	5794	1605	607	1562	35
R. selenitireducens ATCC BAA-1503	Gs0015051	49.77	4780	0.6	4714	66	6	46	3586	882	4107	1211	429	1109	210
R. favelukesii LPU83	Gs0112019	75.70	7785	0.6	7687	98	9	56	4824	1167	5933	1568	582	1581	23
R. taibaishanense DSM 100021	Gs0129175	54.02	4925	0.6	4856	69	4	47	3716	913	4167	1282	376	1148	59
R. alamii LMG 24466	Gs0129175	74.12	7299	0.6	7219	80	2	52	5164	1263	5950	1564	686	1681	41
R. smilacinae CCTCC AB 2013016	Gs0129175	60.06	5775	0.6	5702	73	3	53	4280	984	4867	1399	509	1423	75
R. tropici CF286	Gs0103573	71.42	6824	0.6	6744	80	2	53	4940	1223	5686	1616	609	1606	79
R. hidalgonense FH14	Gs0135555	72.55	7079	0.6	7001	78	3	51	4856	1209	5700	1541	627	1605	12
R. rhizoryzae DSM 29514	Gs0129175	48.62	4616	0.6	4546	70	3	50	3506	886	3929	1235	377	1062	29
R. marinum MGL06	Gs0111130	50.62	4965	0.6	4900	65	3	43	3634	882	4162	1251	432	1187	111

(continued)

Table 20.1 (continued)

Genomes	GOLD ID	Size (/10)	Genes	GC	CDS	RNAs	rRNA	tRNAs	COGs	KOG	Pfams	Enzymes	SP	TMH	HTG
R. yanglingense LMG 19592	Gs0129175	71.76	7032	0.6	6945	87	4	55	5030	1269	5798	1603	601	1593	22
R. paknamense DSM 100301	Gs0129175	53.09	4799	0.6	4718	81	4	54	3577	901	4052	1242	380	1109	87
R. pisi DSM 30132	Gs0129175	69.36	6780	0.6	6705	75	2	51	4828	1226	5580	1556	585	1546	22
R. vignae CCBAU 05176	Gs0111133	63.43	6140	0.6	6071	69	5	45	4487	1069	5139	1459	545	1418	77
R. anhuiense C15	Gs0135555	70.67	6808	0.6	6732	76	3	49	5051	1248	5753	1609	615	1594	18
R. nepotum 39/7	Gs0119505	53.25	5068	0.6	4996	72	3	46	3902	913	4356	464	442	1217	32
R. mesoamericanum DSM 28449	Gs0129175	63.53	6267	0.6	6193	74	3	48	4306	1101	5016	1437	509	1416	31
P. mediterranea CFBP 5447	Gs0030206	63.09	5737	0.6	5536	201	3	54	4025	1107	4759	1399	569	1227	37
P. pertucinogena DSM 18268	Gs0015051	30.65	2928	0.6	2863	65	4	48	2194	628	2527	940	280	738	251
P. pelagia CL-AP6	Gs0030222	46.42	4348	0.6	4260	88	3	46	3042	835	3681	1131	429	1066	966
P. taiwanensis SJ9	Gs0030418	62.53	5600	0.6	5518	82	12	68	3288	867	4361	1277	512	1094	44
P. flexibilis JCM 14085	Gs0115713	37.48	3553	0.7	3467	86	6	58	2695	766	3120	1044	358	862	30
P. guariconensis LMG 27394	Gs0114533	50.79	4741	0.6	4618	123	14	60	3547	981	4085	1300	510	1079	18
P. amygdali pv. lachrymans 107	Gs0117564	73.09	7087	0.6	6945	142	2	84	3901	968	4795	1400	682	1407	0
P. asturiensis sp. nov LMG 26898	Gs0114533	61.74	5666	0.6	5540	126	7	58	3961	1046	4731	1430	569	1266	45
P. paralactis DSM 29164	Gs0118325	60.14	5615	0.6	5348	267	10	56	3880	1007	4554	1346	606	1217	19
P. furukawaii KF707	Gs0030226	66.78	6211	0.7	6111	100	27	73	4295	1208	5171	1499	599	1314	169
P. xinjiangensis CCTCC 207151	Gs0114533	35.37	3352	0.6	3278	74	9	50	2544	720	2909	990	338	851	213
P. rhodesiae	Gs0113582	60.50	5553	0.6	5420	133	9	58	3939	1010	4640	1363	602	1267	46
P. thivervalensis DSM 13194	Gs0119845	65.80	5971	0.6	5731	240	13	58	4304	1120	4988	1458	622	1301	0
P. otitidis LMG 23769	Gs0114533	63.45	5879	0.7	5779	100	6	54	4157	1094	4943	1400	721	1292	51
P. aeruginosa Pae221	Gs0117356	62.83	5869	0.7	5751	118	3	57	4431	1176	5070	1487	699	1393	0
P. benzenivorans DSM 8628	Gs0114533	57.43	5305	0.7	5188	117	6	60	3794	1054	4549	1397	553	1202	254

P. aeruginosa ATCC 700888	Gs0030008	67.95	6423	0.7	6367	56	3	53	4388	1145	5404	1593	693	1429	43
P. aeruginosa JD322	Gs0118288	61.77	6523	0.7	6435	88	5	27	4030	1005	5385	1635	665	1460	1
P. alkylphenolia KL28	Gs0000556	0.08	7	0.6	7	0	0	0	4	1	5	1	0	2	0
P. composti CECT 7516	Gs0114533	53.92	5040	0.6	4928	112	8	56	3731	946	4328	1289	591	1205	43
P. oryzihabitans H72	Gs0120401	53.16	5005	0.7	4897	108	14	58	3641	952	4214	1313	496	1138	8
P. simiae DSM 18861	Gs0114533	62.40	5814	0.6	5687	127	12	54	4264	1107	4932	1444	660	1321	21
P. azotoformans LMG 21611	Gs0114533	67.27	6256	0.6	5997	259	16	68	4542	1201	5261	1533	747	1423	24
P. batumici UCM B-321	Gs0115688	65.93	5979	0.6	5833	146	6	53	4199	1127	4987	1475	602	1356	163
P. aeruginosa CIG1	Gs0030008	65.36	6078	0.7	6025	53	3	50	4233	1082	5204	1528	675	1382	55
P. amygdali pv. tabaci str. ATCC 11528	Gs0116387	61.28	5587	0.6	5465	122	8	57	3799	983	4587	1350	554	1218	0
P. avellanae BPIC 631	Gs0030107	58.47	4789	0.6	4757	32	3	29	3230	825	4089	1268	434	1026	22
P. aeruginosa RW72	Gs0120424	64.78	6047	0.7	5922	125	3	55	4511	1184	5174	1478	721	1409	1
P. taetrolens DSM 21104	Gs0118325	49.20	4582	0.6	4479	103	8	59	3485	991	3945	1316	429	1055	0
P. pseudoalcaligenes CECT 5344	Gs0030225	46.56	4378	0.6	4314	64	3	61	3104	801	3789	1170	384	960	187
P. antarctica LMG 22709	Gs0114533	63.77	6038	0.6	5796	242	18	67	4150	1075	4918	1419	641	1321	50
A. beijerinckii DSM 1041	Gs0103574	50.84	4951	0.7	4824	127	8	53	3150	889	4033	1326	397	893	361
A. beijerinckii DSM 282	Gs0103574	49.15	4872	0.7	4756	116	6	54	3076	854	3928	1271	386	893	362
A. beijerinckii DSM 373	Gs0103574	50.72	4987	0.7	4870	117	5	53	3183	895	4084	1318	396	911	419
A. beijerinckii DSM 378	Gs0103574	49.40	4719	0.7	4598	121	4	54	3117	868	3906	1295	391	905	357
A. beijerinckii DSM 381	Gs0103574	49.23	4865	0.7	4748	117	6	53	3096	868	3928	1277	378	903	358
A. chroococcum DSM 2286	Gs0131304	48.60	4631	0.7	4515	116	6	55	3107	853	3840	1231	399	965	95
A. chroococcum NCIMB 8003	Gs0001478	51.92	4871	0.7	4728	143	18	67	3269	854	3992	1283	413	964	278
A. vinelandii CA	Gs0001480	53.66	5147	0.7	5048	99	18	64	3485	955	4150	1326	395	976	4
A. vinelandii CA6	Gs0001481	53.23	5105	0.7	5006	99	18	64	3453	952	4113	1320	388	962	4
A. vinelandii DJ, ATCC BAA-1303	Gs0001479	53.65	5133	0.7	5051	82	18	64	3441	954	4149	1325	395	976	1140
A. vinelandii DSM 279	Gs0103574	54.85	5230	0.7	5099	131	11	55	3538	954	4402	1353	433	1026	116
A. vinelandii NBRC 13581	Gs0001482	51.30	4872	0.7	4761	111	5	50	3399	934	4099	1294	423	989	34

(continued)

Table 20.1 (continued)

Genomes	GOLD ID	Size (/10)	Genes	GC	CDS	RNAs	rRNA	tRNAs	COGs	KOG	Pfams	Enzymes	SP	TMH	HTG
B. acidiproducens DSM 23148	Gs0015051	33.20	3425	0.4	3278	147	18	73	2249	675	2792	969	135	839	68
B. aerophilus C772	Gs0115005	37.53	3917	0.4	3808	109	19	61	2683	737	3315	1081	186	1062	3
B. aidingensis DSM 18341	Gs0015051	44.20	4531	0.5	4413	118	13	57	2982	834	3662	1178	255	1131	170
B. akibai JCM 9157	Gs0105906	47.40	5021	0.4	4861	160	19	94	2791	751	3871	1279	280	1367	47
B. alcalophilus ATCC 27647	Gs0001513	42.18	4095	0.4	4063	32	2	30	2697	702	3388	1076	166	1105	157
B. altitudinis 41KF2b	Gs0001515	36.79	3800	0.4	3745	55	3	52	2643	719	3259	1070	257	1059	3
B. alveayuensis 24KAM51	Gs0113108	67.02	6828	0.4	6685	143	13	88	4542	1319	5681	2001	162	1627	72
B. amyloliquefaciens 11B91	Gs0120820	40.24	4025	0.5	3904	121	15	75	2730	792	3386	1084	186	1029	3
B. amyloliquefaciens plantarum	Gs0104006	39.92	4170	0.5	4060	110	3	80	2664	766	3452	1146	185	1062	3
B. andreraoultii KW-12	Gs0002052	40.44	3897	0.4	3766	131	25	88	2400	684	3083	915	88	999	0
B. anthracis 2,000,031,006	Gs0118987	54.35	5856	0.4	5756	100	8	66	3272	886	4612	1242	235	1726	0
B. aquimaris	Gs0002052	44.23	4533	0.5	4386	147	19	84	2799	782	3604	1092	182	1242	35
B. aryabhattai B8W22	Gs0001585	50.95	5351	0.4	5232	119	6	78	3363	983	4292	1296	318	1516	13
B. atrophaeus 1013-1	Gs0001587	41.26	4213	0.4	4115	98	3	66	2783	817	3474	1153	262	1105	0
B. aurantiacus DSM 18675	Gs0015051	40.25	4094	0.4	3991	103	17	71	2583	731	3231	1037	232	1160	57
B. australimaris NH7I_1	Gs0120219	36.44	3740	0.4	3675	65	2	37	2645	739	3232	1067	184	1024	3
B. azotoformans LMG 9581	Gs0001602	42.23	4255	0.4	4226	29	4	25	2652	704	3487	1090	266	1128	386
B. badius DSM 30822	Gs0115022	40.64	4210	0.4	4068	142	22	89	2640	747	3328	1038	158	1065	20
B. bataviensis LMG 21833	Gs0001603	53.71	5236	0.4	5207	29	6	23	3534	1013	4453	1387	282	1448	317
B. beveridgei MLTeJB	Gs0113225	35.82	3469	0.5	3363	106	22	67	2451	657	2890	972	117	900	53
B. bingmayongensis FJAT-13831	Gs0001891	54.72	5667	0.4	5546	121	11	83	3331	922	4528	1265	335	1521	24
B. bogoriensis ATCC BAA-922	Gs0015051	50.02	4950	0.4	4822	128	27	71	3027	772	3869	1180	291	1427	148
B. bombysepticus Wang	Gs0110388	58.74	5884	0.4	5724	160	39	95	3487	964	4688	1310	267	1690	7
B. boroniphilus JCM 21738	Gs0105907	43.65	5420	0.4	5294	126	7	77	2148	514	3957	1404	246	1346	4
B. butanolivorans AFS003229	Gs0133685	58.68	5756	0.4	5652	104	4	64	3646	1107	4581	1412	192	1460	9
B. camelliae 7578-1	Gs0135640	49.46	5109	0.4	5023	86	4	56	3054	830	3932	1159	148	1277	68

B. campisalis SA2-6	Gs0116372	51.82	5300	0.5	5062	238	81	116	3410	1026	4239	1380	235	1380	66
B. caseinilyticus SP	Gs0110196	58.73	5337	0.5	5199	138	12	101	3352	774	4164	1299	223	1517	175
B. cecembensis DSM 21993	Gs0116134	47.32	4834	0.4	4735	99	4	46	2840	765	3679	1004	198	1303	36
B. cellulasensis NIO-1130	Gs0119568	36.13	3779	0.4	3684	95	14	53	2637	723	3228	1063	176	1043	0
B. cellulosilyticus N-4, DSM 2522	Gs0018994	46.82	4443	0.4	4327	116	30	81	2673	691	3431	1054	237	1316	340
B. cereus #17	Gs0118079	58.39	5996	0.4	5834	162	38	92	3567	934	4745	1320	263	1713	2

Abbreviations: *R.—Rhizobium*; *P.—Pseudomonas*; *A.—Azotobacter*; *B.—Bacillus*; SP—signal peptides; TMH—transmembrane helices; HTG—horizontally transferred genes

Table 20.2 Genomic perspective of some plant-beneficial PGP microbes

PGPR	Genome size (Mb)	Host plant	PGP traits
Azoarcus sp. BH72	4.37	Rice	N_2 fixation
Azospirillum lipoferum 4B	6.85	Rice, maize, wheat	N_2 fixation, phytohormone
Azospirillum sp. B510	7.6	Rice	N_2 fixation, phytohormone
Burkholderia phytofirmans PsJN	8.2	Potato, tomato, maize, barley	IAA synthesis, ACC deaminase
Burkholderia sp. KJ006	6.6	Rice	ACC deaminase, antifungal action
Enterobacter cloacae ENHKU01	4.7	Pepper	Unknown
Enterobacter sp. 638	4.67	Poplar	Siderophore, IAA, acetoin and 2,3-butanediol synthesis
Gluconacetobacter diazotrophicus PaI5	3.9	Sugarcane, rice, coffee, tea	N_2 fixation, auxin synthesis
Klebsiella pneumoniae 342	5.9	Maize, wheat	N_2 fixation
Pseudomonas putida W619	5.77	Poplar	IAA synthesis, ACC deaminase
Pseudomonas stutzeri A1501	4.5	Rice	N_2 fixation
Serratia proteamaculans 568	5.5	Soybean	IAA synthesis, ACC deaminase, acetoin and 2,3-butanediol synthesis
Stenotrophomonas sp. KA1	4.57	Poplar	IAA synthesis, ACC deaminase
Stenotrophomonas maltophilia R551-3	4.67	Poplar	IAA synthesis, ACC deaminase
Rhizobium leguminosarum	5.5	Pea	N fixation, phytohormone
Citrobacter freundii	5.9	Rice	Phytohormone, IAA synthesis

Source: Ashraf et al. (2004), Krause et al. (2006), Yan et al. (2008), Taghavi et al. (2009), Kaneko et al. (2010), Weilharter et al. (2011), Liu et al. (2013)

stresses. PGPB helps in mounting niche in the expansion of organic agriculture. The benefits done by PGP bacteria to the agriculture are enormous. Numerous genetically engineered PGP bacteria are already being used successfully in a number of countries in the developing world commercially as adjuncts to agricultural practice. The use of detailed molecular techniques and next-generation OMICS-based tools is still to be implemented to study elaborate biochemical and molecular functions of the plant-beneficial microbes. Integrated use of genomics, proteomics, transcriptomics, metabolomics, and secretomics might help biologists to gain better insight into the ecophysiological aspects and niche adaptation strategies of PGP microbes. In spite of all odds, commercialized and more efficacious strains of *Azotobacter*, *Bacillus*, *Paenibacillus*, *Pseudomonas*, and various *Rhizobia* sp. are showing promising development in the field of inoculation. So, study on microbes and their interaction

with plants on commercial scale is still required to make PGPB an efficient technique in agricultural sustainability and intensive production practices.

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