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Microbial Rhizobacteria-Mediated Signalling and Plant Growth Promotion

G. Karthikeyan, L. Rajendran, M. Suganyadevi and T. Raguchander

Abstract

Bacteria are the most abundant microorganisms in soil compared to fungi and other microbes. They play a major role in maintaining soil fertility and plant growth. The rhizosphere is the region of soil that is directly influenced by root exudates of plants and associated with several soil microbes. The root exudates offer carbon-rich nutrients to the microbes, which in turn promotes plant growth indirectly and has a significant role in chemotaxis and biofilm formation. The relationship creates a symbiotic association between plants and microorganisms as a beneficial role such as atmospheric nitrogen fixation, increasing the availability of plant nutrients as well as water, root architecture modification, phytohormone production, microbial volatile production and induced systemic resistance (ISR). During the tripartite (plant-pathogen-rhizobacteria) interaction, different signalling pathways, viz. jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) are activated, which ultimately results in enhanced systemic resistance. JA regulates plant defence through intricate crosstalks with diverse signalling networks manipulated by other phytohormones such as salicylic acid (SA), ethylene (ET) and nitric oxide (NO). The role of non-secondary metabolites, volatile organic compounds and phytohormones in plant growth promotion and inducing resistance is discussed in the chapter.

Keywords

PGPR · Rhizosphere · Volatiles · Plant growth promotion · Rhizobacteria · Systemic resistance

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3.1 Introduction

Bacteria are the most abundant microorganisms in the soil and play a major role in soil fertility. They are approximately 10^{30} on earth, which contributes the biggest fraction of prokaryotic cells (Whitman et al. 1998). The stable temperature and relative humidity in soil matrices create a favourable niche for their survival (Lavelle and Spain 2001). A niche rhizosphere is a specific term coined by Hiltner (1904), found around root region (1–2 mm zone) with rich nutrients of root exudates and attracts microorganisms especially rhizobacteria, which promotes plant growth indirectly. Root exudates offer carbon-rich nutrients to the rhizosphere microorganisms. These organic acids such as citrate, malate, succinate, pyruvate, fumarate, oxalate and acetate and sugars such as glucose, xylose, fructose, maltose, sucrose, galactose and ribose constitute the main course, whereas variable amounts of α-amino acids, nucleobases and vitamins such as thiamin and biotin provide the entry or dessert (Baker and Snyder 1965; Lugtenberg and Bloemberg 2004). The establishment of microbial contact in the rhizosphere region has revealed the significant role of chemotaxis, flagellar motility, lipopolysaccharide (LPS) structure, the outer membrane protein OprF and pili (Lugtenberg and Bloemberg 2004). This relationship creates a symbiotic association between plants and microorganisms as a beneficial, neutral and also some have a harmful effect (Dobbelaere et al. 2003). In the harmful effect, phytotoxic substances as well as pathogenic activities can also be produced by microorganisms which may affect the growth of the plants. In case of beneficial role, atmospheric nitrogen fixation in leguminous plants, increase in the availability of plant nutrients as well as water, root architectures modification, phytohormonal production, microbial volatile production and induced systemic resistance have been documented. However, during the pathogen interaction, the resistance mechanism is developed, which was proved in various soil-borne and foliar pathogens. To enhance the plant yield and maintenance of immune system, plant growth-promoting rhizobacteria (PGPR) play an important role. This can be achieved by specific PGPR strains (Alstram 1991; Van peer et al. 1991; Wei et al. 1991). The PGPR interaction with plants has been commercially exploited in sustainable agriculture (Podile and Kishore 2006). The focus of this chapter is to provide an overview on rhizobacteria-mediated signalling and growth promotion in plants.

3.2 Soil Microflora and Rhizosphere

Soil matrix is relatively very stable in both temperature and humidity (Lavelle and Spain 2001), but different geographical location, soil structure, texture, particle size, composition, mineral nutrient and agricultural practices determine the microbial community. The microbes in the root zone are rich when compared to the bulk soil (Van Loon and Baker 2003), and the viability of cells strongly depends upon the water content of the soil matrices (Normander et al. 1999; Pedgley 1991). The population in the rhizosphere region (rhizocompetence) is determined by various factors which include soil pH, water content, mineral and nutrient status of soil (Albareda et al. 2006). The PGPR are a group of saprophytic free-living bacteria that lives in the rhizosphere of plant and actively colonize the roots. These PGPR have been studied as plant growth promoters and used for increasing production in agricultural and horticultural crops and also used as biocontrol agents against plant diseases. They survive in seed or soil, multiply in the spermosphere in response to seed exudates rich in carbohydrates and amino acids (Kloepper et al. 1992) attach to root surface (Suslow 1980). PGPR, namely *Bacillus subtilis* (Ryu et al. 2003; Xie et al. 2009; Kwon et al. 2010; Zhang et al. 2009; Meldau et al. 2013), *Bacillus megaterium* (Gutiérrez-Luna et al. 2010), *Bacillus vallimortis* (Ann et al. 2013), *Bacillus amyloliquefaciens* (Hao et al. 2016; Asari et al. 2016), *Arthrobacter agilis* (Velázquez-Becerra et al. 2011; Castulo-Rubio et al. 2015), *Paenibacillus polymyxa* (Lee et al. 2012), *Burkholderia ambifaria* (Groenhagen et al. 2013), *Proteus vulgaris* (Bhattacharyya et al. 2018), *Pseudomonas fluorescens* (Park et al. 2015) and *Pseudomonas simiae* (Vaishnav et al. 2015), are involved in plant growth promotion (increase in root and shoot biomass as well as chlorophyll content). A root glycoprotein complex called agglutinin is involved in the short term adherence of pseudomonads (Glandorf et al. 1994). Intensive research work on the establishment of microbial contact with rhizosphere region has revealed the significant role of chemotaxis, flagellar motility, lipopolysaccharide (LPS) structure, the outer membrane protein OprF and pili in successful colonization (Lugtenberg and Bloemberg 2004).

3.3 Non-secondary Metabolites

The production of non-secondary metabolites has been linked to biocontrol (Maurhofer et al. 1994; Thomashow and Weller 1998; Paulsen et al. 2005). The non-secondary antifungal metabolites have been described in *Pseudomonas*. Nielsen and Sørensen (1999) identified a cell surface molecule with biosurfactant property and antifungal activity. Biochemical analysis of the compound showed it to be a newly described bacterial cyclic lipopeptide designated viscosinamide, which has subsequently been implicated in the control of *Pythium ultimum* (Thrane et al. 1999). HPLC analysis of antibiotics showed that small but significant amount of lipopeptide viscosinamide present in the rhizosphere soil inoculated with PGPR strains (Thomashow et al. 1997; Haas and Keel 2003). Paulsen et al. (2005) reported novel antibiotic compounds, namely cyclic lipopeptide or glutamic acid, polyketide and non-ribosomal peptides from the *P. fluorescens* strain Pf5.

3.4 Volatiles in Signalling

Microorganisms produce a wide range of volatile compounds to induce growth in plants directly or indirectly (Dotaniya and Meena 2015) upon the application of biological control agents (BCAs). Their secondary metabolites are important in plant disease management. Ryu et al. (2003) first reported that the volatile organic compounds (VOCs) released by *B. subtilis* GB03 can regulate growth, nutrition and stress in *Arabidopsis thaliana*. These compounds act as a signal molecule having properties of low molecular weight, low boiling point and high vapour pressure and lipophilic nature. It has also been found that certain plants can release stress signals during pest attack, and these can cause defence responses in intact plants (Turlings et al. 1990). The induction of jasmonic acid enhanced the predation rates by triggering the release of airborne volatiles that attract the natural enemies of insect herbivores (Thaler et al. 2001). It can able to change physiological processes and carried through the water, air and soil (Kanchiswamy et al. 2015). Volatiles from attacked plants, microbes and herbivores can enhance plant defences. Depending on the living environment, through different metabolic pathways, VOCs are released from a different group of alcohols, alkanes, esters, alkenes, terpenoids, sulphur families and ketones (Audrain et al. 2015; Korpi et al. 2009; Schulz and Dickschat 2007). Identification of bioactive microbial compounds was done by gas chromatography coupled with mass spectrometry (Korpi et al. 2009). Volatile compounds involve four principles like hormonal balances, sugar concentrations, metabolism and inflection of essential nutrients in seedlings of the plant during cellular and physiological effects (Zhang et al. 2007). Iron element is a demanding essential micronutrient for the photosynthesis (Kim and Guerinot 2007; Waldvogel-Abramowski et al. 2014). Exposure of seedlings to dimethyl hexadecylamine (VOC of rhizobacteria) leads to uptake of iron which provides increased chlorophyll content and also photosynthetic activity as reported in *A. thaliana* by *B. subtilis GB03* (Zhang et al. 2009) and *Medicago truncatula* by *A. agilis* UMCV2 (del Carmen Orozco-Mosqueda et al. 2013) (Fig. 3.1). Additionally, VOCs of *B. amyloliquefaciens* strain BF06 activate gene at molecular level encoding for sulphate transportation and increase in Se accumulation (Wang et al. 2017). Six isolates of *B. subtilis* (B1, B6, B28, B40, B99 and B108) were evaluated against *Fusarium oxysporum* f. sp. *ciceris* of chickpea under in vitro and in vivo. Some isolates showed greater antifungal activity and were found to produce protease, siderophore, indole acetic acid, antifungal volatiles and other extracellular compounds (Karimi et al. 2012) (Table 3.1). It has been provided that volatiles can modulate different hormonal pathways, including jasmonate (JA), salicylic acid (SA), ethylene (ET) and auxin (IAA) signalling. Many of these pathways interact with each other through crosstalk mechanisms.

3.5 Jasmonates (JA)-Mediated Signals

Plants employ JA-mediated defence to defend against various microbial pathogens, and its synthesis was rapidly triggered both locally at the injured site and systemically in undamaged leaves throughout the plants upon pest chewing and wounding by the herbivory (Yan and Xie 2015). Exogenous methyl jasmonate (MeJA) application enhanced the host resistance to parasitic root-knot nematodes

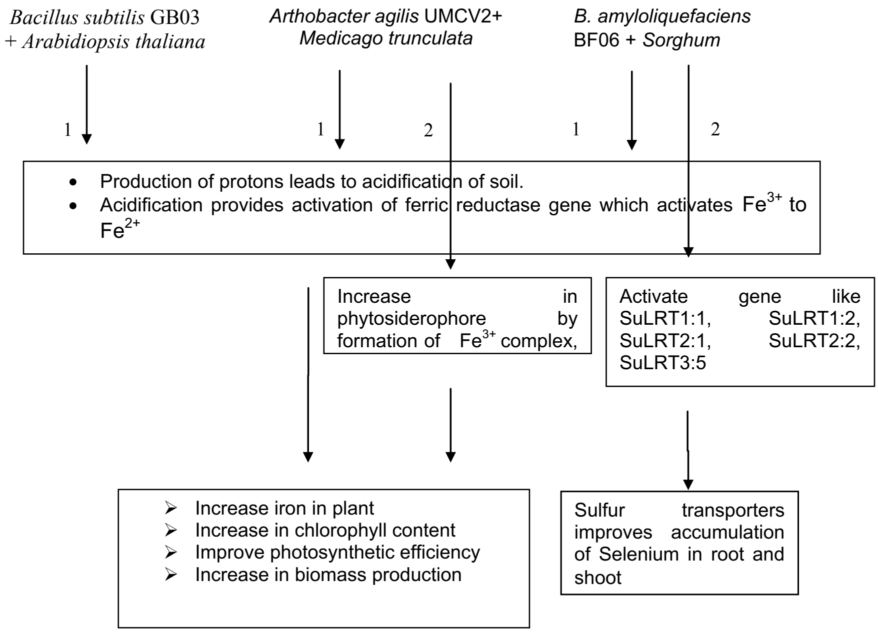


Fig. 3.1 Outline of action 1 and 2 involved in growth promotion of host. FRO1 = Ferric reductase, IRT1 = Iron-regulated transporter 1 and SULRT = Sulphur transporter

(RKNs) in tomato (Cooper et al. 2005). Some JAs can be released as VOCs to permit communication between plants in anticipation of mutual dangers. In addition, JA crosstalk occurs with salicylic acid (SA) which mediates systemic acquired resistance (SAR). JA, salicylic acid (SA) and ethylene signal pathways are integrated into the regulation of stress response and plant development.

3.6 Salicylic Acid (SA)-Mediated Signals

Salicylic acid (SA) is a hormone, mediates defence against pathogens by inducing pathogenesis-related genes and SAR mechanism. It is an essential signal elicitor for the induction of induced systemic resistance (ISR) and the orchestration of the events that occur during the hypersensitive reaction (HR). Shanmugam and Narayanasamy (2008) reported the production of SA in *Bacillus licheniformis* MML2501 from the experiments conducted under in vitro and in vivo. Under optimal pH, temperature, concentration of substrate and shaken conditions, *B. licheniformis* MML2501 showed maximum production of 18 µg/mL of SA, which is an important component in the induction of plant-mediated defence enzymes. Zhang et al. (2002) reported that plants treated with *Bacillus pumilus* strain Se34 had greatly increased levels of SA, compared with that of non-treated

Table 3.1 List of volatile organic compounds (VOCs) of PGPR and its function in the crop

Host	PGPR stains	Volatile compounds	Function(s)	References
Arabidopsis thaliana	*Bacillus subtilis* GB03	2,3-Butanediol	Surface leaf area	Ryu et al. (2003)
	B. megaterium XTBG-34	2-Pentylfuran	Fresh weight	Zou et al. (2010)
	B. pyrrocinia Bcc171	Indole 1-Hexanol pentadecanol	Fresh weight	Blom et al. (2011)
	Bacillus sp. B55	Dimethyl sulphide	Lateral root numbers	Meldau et al. (2013)
	B. ambifaria	Dimethyl disulphide acetophone	Biomass	Groenhagen et al. (2013)
Medicago sativa	*Arthrobacter agilis* UMCV2	Dimethyl hexadecylamine	Fresh weight, stem length, root length, lateral root density	Velazquez-Beceria et al. (2011)
Tobacco	*B. vallismortis* EXT-1	3-Hydroxy-2-butane	Fresh weight	Ann et al. (2013)
	Pseudomonas fluorescens SS101	13-Tetradecadien-1-ol, 2-Methyl-n-1 trideione, 2-Butanone	Fresh weight	Part et al. (2015)
Turmeric	*P. fluorescens*	Induced defence enzymes	Plant height, stem girth and number of leaves	Prabhukarthikeyan et al. (2018)
Tomato	*P. fluorescens* (Pf1)	Induced defence enzymes	–	Manikandan and Raguchander (2014)
Gerbera	*Bacillus subtilis* strain Bbv 57	Butanedioic acid, hexadecanoic acid, pentanedioic acid 2-oxo-dimethyl ester	Increase in number of flowers	Ramyabharathi et al. (2018)

plants or plants treated with two Gram-negative bacteria. *B. subtilis* produces a catecholate, trilactone, siderophore, bacillibactin (BB), under conditions of iron limitation (May et al. 2001).

3.7 Ethylene (ET) in Signalling

It is a simple two-carbon atom molecule, a gaseous plant hormone. Its precursor, 1-aminocyclopropane-1-carboxylic acid (ACC), can be metabolized using ACC deaminase by the bacteria, favouring plant growth and lowering the stress susceptibility (Van de Poel and Van Der Straeten 2014). ACC has been reported to function as a signal itself independently from ethylene. Some PGPRs are capable of converting plant-borne ACC into ammonia and α-ketobutyrate by ACC deaminase enzyme reported in *Pseudomonas chlororaphis* 6G5 (Klee et al. 1991), *Pseudomonas putida* GR12-2 (Jacobson et al. 1994) and *P. putida* UW4 (Hontzeas et al. 2004). Saravanakumar and Samiyappan (2007) reported that the PGPR *P. fluorescens* strain TDK1 possessing ACC deaminase activity enhanced the saline resistance in groundnut plants, which in turn resulted in increased yield when compared with the groundnuts treated with *Pseudomonas* strains not having ACC deaminase activity. The bacterial ACC deaminase can reduce the endogenous ethylene levels of plant roots by limiting the amount of available ACC, which will in turn prevent ethylene-induced root growth inhibition, and thus promote plant growth (Glick 2014). Xu et al. (2014) reported that *B. subtilis* (HYT-12-1) exhibited multiple plant growth-promoting (PGP) traits, namely 37% of indole-3-acetic acid production; 37% of phosphate solubilization; 24% of siderophores production; 85% of potential nitrogen fixation; and 6% of 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity.

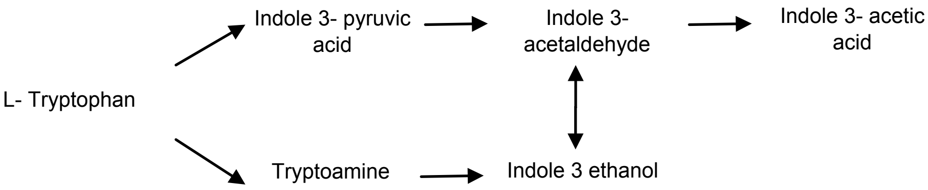
3.8 Auxin (IAA)

The auxin word has been derived from Greek means auxein, regulate a plant developmental process and best documented in PGPR, *Azospirillum* spp (Persello-Cartieaux et al. 2003; Spaepen et al. 2007), which regulates plant root development. This is chemically called as indole acetic acid (IAA) and act as signalling in defence response in the *Arabidopsis* against a foliar pathogen (Navarro et al. 2006). Almost, 80% of bacteria isolated from rhizosphere region can able to produce IAA (Patten and Glick 1996; Khalid et al. 2004) by the main precursor L-tryptophan, which is secreted in root region. The hormone acts as a signal molecule in bacteria and effector molecule in plants. Bacteria synthesize auxins in order to perturb host physiological processes for their own benefit (Yung 2010). PGPR possess different pathways for synthesis of (a) by indole-3-pyruvic acid in the case of *Rhizobium, Bradyrhizobium* and *Azospirillum* (Burdman et al. 2000; Costacurta and Vanderleyden 1995; Manulis et al. 1991; Patten and Glick 1996) (b) via tryptamine pathway by *B. subtilis*, *B. megaterium*, *B. licheniformis*, etc. Damodaran et al. (2013) reported that two stress-tolerant rhizobacteria, *B. pumilus* B-1 and *B. subtilis* B-3, had extensive zone formation for indole-3-acetic acid (>1 cm) and siderophore production with higher zone ranging from 0.6 to 0.9 cm. Mohite (2013) reported that the production of IAA was maximum in the tryptophan-amended medium. Indole-3-acetic acid stimulates cell elongation by modifying certain conditions like increase in osmotic contents of the cell, increase in permeability of water into the cell, decrease in wall pressure and an increase in cell wall synthesis and protein synthesis. It inhibits or delays abscission of leaves and induces flowering and fruiting (Zhao 2010). The microorganisms isolated from rhizosphere region of various crops have an ability to produce IAA as a secondary metabolite due to the rich supply of substrates (Table 3.2). IAA helps in the

Table 3.2 Illustrations of plant auxin signalling upon colonization by PGPRs

PGPR strain	Host plant	Phytohormone	Mechanism	References
Azospirillum	Wheat	Auxin-IAA	Increased rooting	Dobbelare et al. (1999)
Pseudomonas putida $GR_{12\text{-}2}$	Canola	Auxin-IAA	Root elongation	Xie et al. (1996)
Rhizobium	Legume-Pea	Auxin-IAA	Root nodule formation	Badenochjoner et al. (1983), Theunis et al. (2004)
Sphingomonas sp. LK11	Tomato	Gibberellin	Shoot elongation	Spaepen and Vanderleyden (2011), Khan et al. (2014)
Rhizobium phaseoli	*Graminaea*	GA1, GA3	Plant growth yield	Bastial et al. (1998)
B. pumilis, *B. licheniformis*	Alnus glutinosa	GA, GA3, GA4, GA20	Growth promotion	Gutierrez-Monero et al. (2001)
Acinetobacter calcoaceticus	Cucumber	GA	Higher shoot length, plant biomass, chlorophyll	Kang et al. (2012)

production of longer roots with an increased number of root hairs and root laterals which are involved in nutrient uptake (Datta and Basu 2000).



According to Dobbelaere et al. (1999), *Azospirillum* alters IAA production, which leads to increased rooting by the enhancement of root exudation and plant mineral, which in turn stimulates bacterial colonization (Steenhoudt and Vanderleyden 2000; Lambrecht et al. 2000). Similarly, *P. putida* GR12-2 stimulates root elongation was shown to the production of IAA (Xie et al. 1996). Root morphology was studied after the application of *Azospirillum,* and it mimicked by IAA (Morgenstern and Okon 1987) or mixtures of GA3, auxin and kinetin (Tien et al. 1979; Hubbell et al. 1979).

3.9 Crosstalks

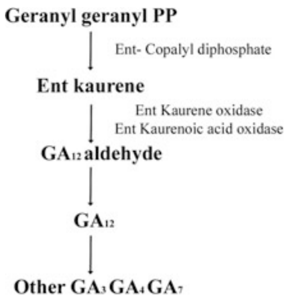
The antagonistic effect of SA on JA signalling was shown to be controlled by a novel function of the defence regulatory protein NPR1 in the cytosol (Spoel et al. 2003). Based on the nature and cause of pathogen, the plant can decide which kind of strategy can be used for crosstalk between defence signalling pathways. De Vos et al. (2005) established the dynamics of SA, JA and ET signalling in a single plant species of *A. thaliana* in response to an attack by a range of microbial pathogens and herbivorous insects with very different modes of action. A complex set of transcriptional alterations are induced in all cases showing stress-related genes, and they are overlapped in response to a different mode of attack by pathogens and insects.

3.10 Phytohormones in Signalling

Plant hormones are usually found in small amount, can be natural or synthetic and defined as an organic substance synthesized in different organs could be translocated to other sites, where it alters morphological, physiological and biochemical processes. These are signal molecules, and chemical messenger in plants promotes its growth and development and regulates intrinsic genetic expression. They are generally classified as auxin, gibberellin, cytokinin, abscisic acid and ethylene. There was a positive correlation between phytohormones produced by PGPR and uptake of soil water and minerals.

3.11 Gibberellin (GAs)

Gibberellins are a major class of important diterpenoid acids (Martin et al. 2000) and are endogenous hormones play a vital role in developmental processes, viz. germination, elongation of stem, dormancy, sex expression and fruit senescence (Eleazar et al. 2000; Gelmi and perez-Correa 2000). Biosynthetic pathway of gibberellin involves precursor geranylgeranyl PP via copalyl diphosphates produce the kaurene and this will be converted into gibberellic acid 12 through a intermediate compound called GA12 aldehyde. Until now, four groups of gibberellic acid like GA1, GA3, GA4 and GA20 were identified from seven bacterial species (Hedden and Thomas 2012). When *Sphingomonas* sp. LK11 strain was inoculated in tomato plants, showed significant results in shoot elongation due to the production of gibberellin (Spaepen and Vanderleyden 2011; Khan et al. 2014). In red pepper, newly identified PGPR were evaluated for growth promotion but also increased endogenous gibberellin level (Joo et al. 2004, 2005). The gibberellin produced by *B. subtilis* strain HC8 (150 ng per 10^9 cells) significantly promoted plant growth and protected tomato against tomato foot and root rot. Gibberellin (approximately 200 ng per 10^9 cells) has been reported from *B. licheniformis* and *B. pumilus* by Manero et al. (2001).

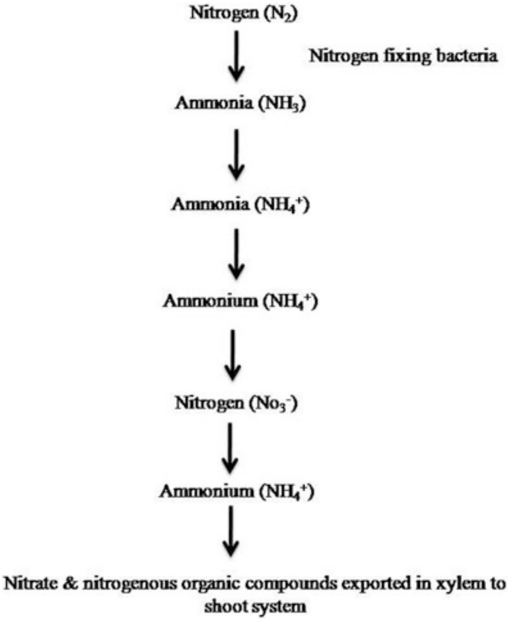


3.12 Cytokinin

In plant cells, cytokinesis process is regulated by one of the PGRs called cytokinin (Skoog et al. 1965). Naturally occurring kinetin (6-furfuryladenine) like compound was isolated from sunflower, maize and soybean (Miller 1961). Pure crystalline form of cytokinin was first isolated from *Zea mays* called as zeatin (Z) by Letham (1967). Plant growth has been directly promoted by PGPR, viz. *Azotobacter*, *Azospirillum* and *Rhizobium* through altering physiological process and production of metabolites (Arshad and Frakenburger 1993). PGPR like *Serratia* (Zhang et al. 1997), *Pseudomonas* (Arshad and Frankenberger 1993; Kloepper 1993) and *Bacillus* (Turner and Blackman 1991; Mariano et al. 1997) play a vital role in the promotion of plant growth. Growth promotion by *Pseudomonas* sp. was first reported by Lifshitz et al. (1987). The most studied PGPR, *Azospirillum,* was isolated from forage, grain and native crops as well as cultivated crops (Magalhães et al. 1983; Dobereiner and Pedrosa 1987; Reinhold et al. 1987; Khammas et al. 1989). When hydroponics media were amended with auxin and cytokinin, depicts morphology of roots were similar to the plants inoculated with *Rhizobium* (Skoog et al. 1965; Puppo and Rigaud 1978). At the root surface, the release of auxin and cytokinin can stimulate cell division in the cortex (Sequeira 1973). Some cytokinins production were observed in PGPR strains, including *Pseudomonas,* and *Serratia* *(*Kloepper et al. 1988) were screened for PGR production and a relationship between induction of root elongation and production (Young et al. 1990).

3.13 Atmospheric Nitrogen Fixation

Nitrogen is the most important gas present in the atmosphere even though it is available around 78%, cannot be utilized directly by plants. Using a complex enzyme system, known as nitrogenase (Kims and Rees 1994), atmospheric nitrogen is converted into ammonia by nitrogen-fixing microorganisms. Biological nitrogen-fixing microorganisms were widely distributed in the atmosphere and survives at mild temperature (Raymond et al. 2004), which serves as an alternative to chemical fertilizer. These organisms are classified into a symbiosis and non-symbiosis group. Symbiosis group includes *Rhizobia* (Ahemad and Khan 2012; Zahran 2001) and *Frankia,* while non-symbiosis bacteria include *Cyanobacteria* (Anabaena, Nostoc), *Gluconacetobacter, Azospirillum* and *Azotobacter* (Bhattacharyya and Jha 2012).



Root exudates of *Alnus glutinosa* (black alder) contain flavonol (quercetin and kaempferol), which enhance the level of nodulation (Hughes et al. 1999). Curling of root hair is the primary event of the symbiotic process, when *Frankia* exposed to *A. glutinosa* root filtrate (Prin and Rougier 1987; Van Ghelue et al. 1997).

3.14 Rhizobacteria-Mediated Growth Promotion

The plant roots are highly influenced the presence of microbial diversity (Bais et al. 2006) that is the availability of nutrient compounds such as simple sugars, organic acids and amino acids in different stages of crop growth. Utilization of these substrates and compounds leads to increased microbial biomass, and activity around the root region is termed as rhizosphere effect (Hartmann et al. 2008). Moreover, the release of specific nutrients from the root zone, which created a fondness for specific bacterial strains, prefers selective colonization (Bowen 1991; Flores et al. 1999; Whipps 2001; Lugtenburg et al. 2002). The root-colonizing bacteria are termed as rhizobacteria, which are confined to root surface, and some of them enter into host maintain symbiotic relationship called as endophytes (Sturz et al. 2000). According to Kloepper et al. (1980), artificial application of beneficial microbes which promote plant growth is called as plant growth-promoting rhizobacteria (PGPR). Physiological modifications as well as a revolution in the microbial communities in the root region create plant growth promotion (directly or indirectly) mechanisms in the host plant (Glick 1995; Glick et al. 1998). These rhizobacteria utilize root exudate which is a mixture of primary and secondary metabolites, cation, mucilaginous substances, enzymes, oxygen and water. In addition, 20–40% of the carbon produced from photosynthesis is utilized by underground root system (Philippot et al. 2013; Venturi and Keel 2016). Many PGPR strains have the ability to induce systemic resistance, produce volatile organic compounds, phytohormones, flavonoids as signals, fixation of atmospheric nitrogen, solubilization of available minerals and biofilm formation. Further, the antimicrobial compounds have other effects at sub-inhibitory concentrations, viz. (a) a role in intercellular signalling and (b) motility and biofilm formation (Davis et al. 2006). Voluminous intelligence between PGPR and plants is recognized by signal molecules of extreme different genera of which *Bacillus* and *Pseudomonas* spp. are predominant.

3.15 Mineral Solubilization

3.15.1 Phosphate-solubilizing Microorganism (PSM)

Minerals are naturally occurring inorganic chemical compound as a solid material and phosphorous play a vital role in the plant growth among 17 nutrients reported. Further, it plays a critical role in photosynthesis, energy transfer, transformation of sugars and starches and transformation of genetic material from one generation to other generation. Acquisition of plant nutrient was enhanced by soil microorganisms. Insoluble forms of phosphatic fertilizer like tricalcium phosphate $(Ca_3PO_4)^2$, aluminium phosphate (Al_3PO_4) and iron phosphate (Fe_3PO_4) were converted into available by microorganisms (Gupta et al. 2007; Song et al. 2008; Khan et al. 2013; Sharma et al. 2013). Wide range of biological process involved in transformation of insoluble nutrients into soluble nutrients (Babalola and Glick 2012). Two types of phosphate utilization were observed like direct application of phosphate fertilizer and microbial solubilization. In the soil, artificial application of phosphatic fertilizers leads to little amount of absorption by plant, and the remaining will be converted into insoluble complexes. These will be solubilized by microorganisms in higher-level conversion (Mckenzie and Roberts 1990) mediated by the enzymes released by the soil microbes called phosphatases (Yadav and Tarafdar 2003; Tarafdar et al. 1988; Aseri et al. 2009) and phytases (Maougal et al. 2014).

Phosphate-solubilizing activity was coupled with organisms which are termed as phosphate-solubilizing microorganism, which provides available forms of phosphorous to the plants (Khan et al. 2006). These bacteria are belonging to the genera, *Azotobacter*, *Bacillus*, *Microbacterium*, *Erwinia*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Flavobacterium*, *Beijernicka*, *Microbacterium* and *Serratia* (Bhattacharyya and Jha 2012). Gram-negative bacteria like *P. fluorescens, Chromobacterium violaceum* and *Pseudomonas aeruginosa* are phosphate-solubilizing bacteria, also secrete antibiotics (Lipping et al. 2008; Taurian et al. 2010) and act against soil-borne pathogens (Khan et al. 2002; Singh et al. 2010; Vassilev et al. 2006). Few genera of *Rhizobium* and *Bradyrhizobium* have also found to solubilize P and also secrete IAA (Badawi et al. 2011; Pandey and Maheshwari 2007). Glick et al. (2007) studied numerous phosphate-solubilizing bacteria which are having the ability to synthesize 1-aminocyclopropane-1-carboxylate (ACC) deaminase, an immediate precursor for the plant hormone ethylene.

3.15.2 Potassium-solubilizing Bacteria (KSB)

Potassium (K) is considered as a major constituent and essential element in all living cells. Naturally, soils contain K in larger amounts than any other nutrients; however, most of the K is unavailable for plant uptake. Depending on soil type, 90–98% of potassium in the soil is in the unavailable form (Sparks and Huang 1985). This can be converted to soluble forms by potassium-solubilizing bacteria for the plant uptake (Etesami et al. 2017) and mostly belong to the genera *Bacillus spp.* having the capacity to solubilize K minerals like feldspar, muscovite, biotite, orthoclase, illite and mica. This can be possible by various processes in conversion of silicate minerals through the process like acidolysis, complexolysis, chelation and exchange of reaction.

Upon artificial inoculation of phosphate-solubilizing bacteria may lead to improve plant growth by increasing seed emergence, plant weight and yield. These include *Pseudomonas* spp., *P. chlororaphis*, *P. aureofaciens*, *P. solanacearum*, *P. syringae*, *P. fluorescens*, *Bacillus* spp., *B. pumilus*, *B. mucilaginous*, *B. amyloliquefaciens*, *B. fimus*, *B. megaterium*, *B. subtilis*, *B. licheniformis*, *Burkholderia cepacia*, *Delftia acidovorans*, *Paenibacillus macerans*, *Pantoea agglomerans*, *A. lipoferum*, *Agrobacterium radiobacter*, *Azospirillum brasilense*, *Serratia entomophilia*, *Azotobacter chroococcum*, *Streptomyces* spp., *S. lydicus* and *S. griseoviridis* (Glick 2012).

Major mechanism involved in conversion of insoluble form into soluble form through formation of organic acids via production of protons (acidolysis mechanism) (Maurya et al. 2014; Uroz et al. 2009; Parmar and Sindhu 2013; Sheng et al. 2003; Meena et al. 2015b; Sheng et al. 2008; Meena et al. 2014). Various organic acids such as tartaric acids, oxalic acid, 2-ketogluconic acid, gluconic acid, succinic acid, citric acid, lactic acid, propionic acid, malic acid, malonic acid, fumaric acid, glycolic acid have been reported in KSB, which are effective in releasing K from K-bearing minerals (Hu et al. 2006; Krishnamurthy 1989; Liu et al. 2012; Prajapati et al. 2013; Keshavarz Zarjani et al. 2013; Saiyad et al. 2015; Prajapati et al. 2012; Sheng and He 2006).

According to Huang et al. (2013), the cation exchange complex was occurring in exchange of hydrogen ions by K^+, Mg^{2+}, Ca^{2+} and Mn^{2+}. In addition to decreasing soil pH, KSB produce organic acid can release K ions from mineral ore by formation of complex structure with Ca^{2+}, Al^{3+}, Si^{4+} and Fe^{2+} with K. Microbial decomposition of organic materials also produces ammonia and hydrogen sulphide that can be oxidized in the soil to form the strong acids such as nitric acid (HNO_3) and sulphuric acid (H_2SO_4). Hydrogen ions displace K^+, Mg^{2+}, Ca^{2+} and Mn^{2+} from the cation exchange complex in a soil (Huang et al. 2013). In addition to decreasing soil pH, organic acids produced by KSB can release K ions from the mineral K by chelating (complex formation) Si^{4+}, Al^{3+}, Fe^{2+} and Ca^{2+} ions associated with K minerals (Römheld and Kirkby 2010; Štyriaková et al. 2003; Meena et al. 2014). When seeds and seedlings were inoculated with KSB, enhancement of germination, increase in K uptake under field condition as well as greenhouse condition have been reported (Zhang and Kong 2014; Anjanadevi et al. 2016; Awasthi et al. 2011; Meena et al. 2014; Subhashini and Kumar 2014; Zhang et al. 2013; Meena et al. 2015a; Lynn et al. 2013). Parmar (2010) observed that inoculation of K-solubilizing isolate HWP47 in wheat cause increase in shoot dry weight as well as root dry weight.

3.16 Siderophores

Siderophore-mediated competition for iron by *Pseudomonas* sp. as well as induced resistance is primary mechanisms shown to be responsible for the suppression of *Fusarium* wilt (Lynch 1990). Vijendra Kumar and Ashok Kumar (2012) reported the production of siderophore in *B. subtilis* WR-W2 and *B. amyloliquefaciens* MR-AI strains under in vitro. Synthesis of siderophore was determined in the presence of iron-limited M9 medium. Siderophore production was inhibited above 20 μM concentration of Fe (III). *P. aeruginosa* strain FP7 was tested for its in vitro antagonistic activity against *Rhizoctonia solani* on King's B media, with and without $FeCl_3$, showed a significant reduction in *R. solani* growth with $FeCl_3$ supplementation compared to the control (without $FeCl_3$) (Sasirekha and Shivakumar 2016). A marine isolate of fluorescent *Pseudomonas* sp. having the ability to produce the pyoverdine type of siderophores under low-iron stress conditions was identified. This *Pseudomonas* culture and purified siderophore showed good antifungal activity against the plant deleterious fungi, viz. *Aspergillus niger*, *Aspergillus flavus*, *Aspergillus oryzae*, *F. oxysporum* and *Sclerotium rolfsii* (Manwar et al. 2004). Though siderophores are part of primary metabolism (iron is an essential element), on occasion they also behave as antibiotics which are commonly considered to be secondary metabolites (Haas and Defago 2005).

3.17 Conclusions

The evidence indicates that JA regulates plant defence through intricate crosstalks with diverse signalling networks manipulated by other phytohormones such as salicylic acid (SA), ethylene (ET) and nitric oxide (NO) (Yan and Xie 2015).

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