

Rhizobacterial Efficacy for Sustainable Crop Productivity in Agroecosystems

Manoj Kaushal

Resilient Dryland Systems, International Crops Research Institute
for the Semi-Arid Tropics (ICRISAT), Hyderabad, India Email:
kaushal.mbg@gmail.com

1. INTRODUCTION

Sustainable agricultural development is best defined as the management and conservation of agricultural resource base in an appropriate, economically viable and socially acceptable way. Thus, sustainable agriculture should ensure availability, access, utilization and stability of resources to present and future generations. However, ecosystem resilience has emerged as a key factor to reach the goal of sustainability. Resilience is defined as the capability of a system to anticipate, absorb, accommodate or recover from the effects of an undergoing change so as to ensure the preservation or restoration of its essential basic structures, identity and functions. There has been substantial increase in the productivity of the crops with the use of chemical inputs to provide nutrition to the crop and to control pests and diseases. However, these have several negative effects like development of pathogen resistance to the applied agents and their non-target environmental impacts, degradation of soil productivity, depletion of non-renewable sources of energy (Prasad et al., 2014) etc. Plant growth promoting rhizobacteria (PGPR) commonly called rhizobacteria, have received prominent attention because of their multifarious activities to improve plant growth and disease control ensuring crop yields in a sustainable way. The application of PGPR to crops offers an environment friendly approach of reducing chemical inputs (Prasad et al., 2005, 2015).

2. RHIZOBACTERIAL CLASSIFICATION AND THEIR PLANT GROWTH MECHANISMS

Rhizobacteria (PGPR) encompass all bacteria that inhabit rhizosphere and they promote plant growth either through direct mechanisms which include production of phytohormones, enhanced availability of nutrients, stress alleviation or by indirect

mechanisms that include suppression of pathogens by antibiosis, synthesis of lytic enzymes and induced systemic resistance (ISR) (Glick, 2012). Bhattacharya and Jha (2012) functionally categorized rhizobacteria as (i) biofertilizers (a substance consisting of live microorganisms having biological nitrogen fixation and phosphorus solubilisation capabilities), (ii) phytostimulators (microorganism with phytohormonal production capability) and (iii) biopesticides (microorganisms controlling phytopathogens). However, based on their location, Gray and Smith (2005) characterized rhizobacteria as extracellular (ePGPRs) and intracellular PGPRs (iPGPRs). Intracellular PGPRs exist inside plant cells and are able to produce specialized nodular structures, whereas ePGPRs colonizing the rhizosphere, the rhizoplane or within the spaces of the root cortex, but not inside the cells. Inoculating crops with rhizobacterial strains has resulted in significant increase in growth and productivity.

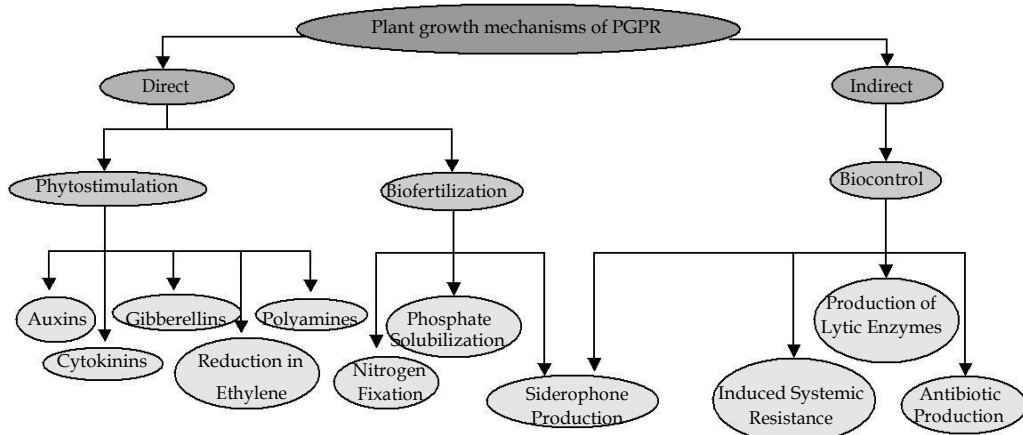


Fig. 3.1 Mechanisms of plant growth promotion exhibited by rhizobacteria

3. PHYTOHORMONAL PRODUCTION

Phytohormonal production by rhizobacteria is among most recognized mechanisms promoting plant growth. It has been reported that the PGPR can stimulate plant growth through production of auxins, gibberellins and cytokinins or by reducing high levels of endogenous ethylene in the plant (Glick, 2012). It has been reported that indole acetic acid (IAA) plays central regulatory roles in apical dominance, lateral root initiation and vascular differentiation. IAA production by PGPR causes modifications in root system architecture by increasing number of root tips and root surface area, thus increasing nutrient acquisition (Mantelin and Touraine, 2004). Different pathways are involved in the biosynthesis of IAA based on the chemical nature of intermediate molecules produced using tryptophan as precursor. However, in Gram-positive bacteria, the main pathway for IAA biosynthesis involves indole-3-pyruvic acid (IPA). PGPR can also stimulate the plant auxin route in an indirect manner. It has been observed that during root colonization by rhizobacterial strains (possessing nitrite reductase activity), NO is produced which

results in lateral root formation as NO is involved in auxin signalling pathway (Molina-Favero et al., 2008). IAA production by rhizobacteria, results in increased root length, root surface (Egamberdieva and Kucharova, 2009). Increased root surface area enables the plant to access more nutrients from soil and thus contributes to plant growth promotion. Plant cell walls get loosened in response to rhizobacterial IAA thus causing an increase in amount of root exudates. Thus, the additional nutrient availability further supports the growth of rhizospheric bacteria (Glick, 2012). Many of the rhizobium species show ability to synthesize IAA and some studies have indicated that auxin plays a key role in the nodulation of legume crops and as a whole, in rhizobium-legume symbiosis. It has been proved that flavonoids (as inducers of nodulation genes) intensify IAA synthesis through rhizobiums. Moreover, it has been shown that compared with roots that don't have nodes, nodular roots contain higher levels of IAA hormone and it plays a role in the development of the root system and its maintenance.

Besides auxins, cytokinins and gibberellins producing rhizobacterial strains have been reported to cause plant growth. Production of gibberellins has been reported in *Achromobacter xylosoxidans*, *Acinetobacter calcoaceticus*, *Azospirillum* sp., *Azotobacter* sp., *Bacillus* sp., *Herbaspirillum seropedicae*, *Gluconobacter diazotrophicus* and rhizobia (Dodd et al., 2010). Fulchieri et al. (1993) showed that application of gibberellic acid on maize at a concentration similar to that produced by *Azospirillum*, promotes root growth due to increased root hair density in root zones.

Cytokinin stimulates cell divisions, cell enlargement, induce root hairs proliferation, but inhibit lateral root formation and primary root elongation. Cytokinin production (especially zeatin) has been reported in *Azospirillum brasilense*, *Bradyrhizobium japonicum*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, and *Paenibacillus polymyxa*. Inoculating plants with rhizobacteria producing cytokinins stimulated shoot growth and reduced the root to shoot ratio (Arkhipova et al., 2007).

In the plant, the higher concentration of ethylene induces defoliation and other cellular processes that trammel crop yield. It has been investigated that certain PGPR strains possess the enzyme ACC deaminase which can cleave the plant ethylene precursor ACC to ammonia and α -ketobutyrate thereby lowers the level of ethylene thus promoting plant growth (Glick, 2012). In addition to a direct role of ethylene on plant growth, this hormone can also act as a virulence factor and a signaling molecule in induced systemic resistance (ISR) against pathogen attack (Van Loon, 2007).

Polyamines are aliphatic nitrogen compounds ubiquitous in bacteria, plants and animals, and are involved in various metabolic and hormonal pathways that regulate plant growth and development as well as plant responses under drought stress (Alcazar et al., 2010). Enhanced root growth caused by cadaverine (polyamine) production promoted growth in *Oryza* seedlings when inoculated with *A. brasilense* Az39 (Cassan et al., 2009). Wheat and maize plants inoculated with *Azospirillum brasilense* strain Az39, produced polyamines, such as spermidine and spermine (Perrig et al., 2007), and putrescine in culture.

4. BIOFERTILIZERS

Biofertilizers are considered an environment-friendly alternative to chemical fertilizers ensuring increased crop productivity. The well-studied PGPR's considered biofertilizers correspond to nitrogen fixation, utilization of insoluble forms of phosphorus and production of siderophores.

4.1 Nitrogen Fixation

Nitrogen is an essential nutrient for all forms of life on the earth. The prokaryotic microbes play an important role in conversion of atmospheric nitrogen (N_2) to available form for plant and microbial growth. Rhizobacteria improve the growth and nitrogen fixation by inducing the occupancy of introduced rhizobia in the nodules of the legume. Inoculating rice with *A. amazonense* increased grain dry matter and nitrogen accumulation. Promotion of growth by *A. amazonense* for rice plants was primarily a response to nitrogen fixation (Rodrigues et al., 2008). Study conducted by Kaushal and Kaushal (2013), reported that most efficient nitrogen fixing isolate *Bacillus pumilus* isolated from cauliflower rhizosphere showed highest nitrogenase activity (437.26 η mole C_2H_4 h^{-1} mg^{-1} protein or about 109 mg of N_2 fixed/ha per day). Islam et al. (2010) also reported the Acetylene Reduction Array (ARA) of free living bacteria in the range of 1.8 η mole C_2H_4 h^{-1} mg^{-1} protein to 2,844.7 26 η mole C_2H_4 h^{-1} mg^{-1} protein.

4.2 Phosphate Solubilization

Phosphate solubilizing bacteria (PSB) can be a viable substitute to chemical phosphatic fertilizers as they help plants to acquire the available forms of phosphorus. Bacterial genera like *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas* and *Rhizobium* are the most significant phosphate solubilizing bacteria (Bhattacharyya and Jha, 2012). PSB in general bring about mobilisation of insoluble phosphates, however their plant growth promoting activities, such as indole acetic acid (IAA), gibberellic acid, cytokinins, ethylene production, hydrogen cyanide (HCN) production, asymbiotic nitrogen fixation and resistance to soil-borne pathogens, etc., have been observed by Cattelan et al. (1999). PSB have been used since long as bio-inoculants for various crops due to their antagonistic and phosphate solubilizing properties. Citrate, lactate, and succinate are various organic acids produced by PSB that solubilise mineral phosphates. Gluconic acid and 2-ketogluconic acid are other active organic acids produced by rhizobacteria which consume the organic acids in root exudates and, therefore, indirectly may moderate solubilisation of P and other immobile elements, such as Fe and Mn.

4.3 Siderophore Production

Siderophores are low molecular weight, iron chelating ligands synthesized by microorganisms that suppress pathogenic microorganisms by limiting iron availability. Under iron-limiting conditions, microorganisms produce a range of iron chelating compounds or siderophores which have a high affinity for ferric ions. These bacterial

iron chelators are thought to sequester the limited supply of iron available in the rhizosphere making it unavailable to pathogenic fungi, thereby restricting their growth. Recent studies clearly revealed that iron nutrition of plant influences the microbial community structure in rhizosphere. Iron competition in *Pseudomonads* has been intensively studied and role of pyoverdinin siderophore produced by many *Pseudomonas* spp. has been clearly demonstrated in the control of fungal pathogen like *Pythium* and *Fusarium* spp. (Duijff et al., 1994). Another siderophore called pseudobactin produced by *Pseudomonads* was responsible for inducing systemic resistance against many fungal diseases (Leeman et al., 1996). *Bacillus subtilis* is the source of the first 2, 3-dihydroxybenzoyl containing substances which have been shown to stimulate uptake of iron. Sharma et al. (2003) suggested that siderophores produced by *Pseudomonas* spp. may be used by the bacteria (homologously) or in effecting plant nutrition (heterologously). The problem of iron non-availability particularly in calcareous soils may be overcome by incorporation of siderophore producing strains of fluorescent *Pseudomonads* (FLPs). Cantero et al. (2007) isolated bacterial strains showing dissimilatory Fe-reducing activity from rhizosphere of bean and maize plants. Isolates were identified as *Bacillus megaterium*, *Arthrobacter* sp. and *Stenotrophomonas maltophilia*. All the isolates showed Fe reduction in alkaline soil and were able to stimulate plant growth. Ahmad et al. (2008) also proved that production of siderophore by PGPR directly influence plant growth promotion. Chakraborty et al. (2006) isolated siderophore producing *Bacillus megaterium* from tea rhizosphere and reported that the bacterial inoculation has reduced disease incidence in tea.

5. BIOLOGICAL CONTROL

In modern input intensive agricultural production system, the indiscriminate use of agrochemicals is posing a chronic threat not only economically, but also ecologically to the entire ecosystem throughout the world. The mechanism of plant growth promoting bacteria as biocontrol agents has become increasingly better understood over the past two decades. Rhizosphere competence of biocontrol agents comprises effective root colonization combined with the ability to survive and proliferate along growing plant roots over a considerable time period, in the presence of indigenous microflora. Studies have shown that plant growth promoting rhizobacteria can be applied to a wide range of plants for the purpose of disease control and growth enhancement (Van Loon et al., 2007). The application of PGPR as biological agent has been recommended to control bacterial wilt of tomato caused by *Ralstonia solanacearum* (Guo et al., 2002), black rot of crucifers caused by *Xanthomonas campestris* pv. *campestris*, root rot of cauliflower caused by *Pythium ultimum* var. *ultimum* (Mariano et al., 2002) and dry rot disease caused by *Fusarium* spp. (Recep et al., 2009). Anith et al. (2004) compared the effectiveness of different strains of *Pseudomonas* (*P. putida* 89B61) and *Bacillus* (*B. pumilus* SE34) to control bacterial wilt caused by *Ralstonia solanacearum* and recommended *P. putida* 89B61 application for effective control under greenhouse condition. Srivastav et al. (2004) recommended the use of phosphate solubilizing bacteria of *Pseudomonas* spp. against a number of plant pathogenic fungi. The application of *Pseudomonas fluorescens* to black pepper is known to enhance root proliferation and fibre root production in addition to act as biocontrol agent

against foot rot caused by *Phytophthora capsici* (Paul and Sharma, 2006). The offensive plant growth promoting bacterial colonization and defensive retention of rhizosphere niches are enabled by production of allelo-chemicals; including antibiotics, iron chelating siderophores, biocidal volatiles, lytic enzymes and detoxification enzymes. Butyrolactones, zwittermycin A, kanosamine, oligomycin A, phenazine-1-carboxylic acid, pyoluteorin, pyrrolnitrin, viscosinamide, xanthobaccin, and 2,4-diacetyl phloroglucinol (2,4-DAPG) are various antibiotics produced by rhizobacterial strains. The 2,4-DAPG is one of the most efficient antibiotics (phloroglucinol compound) having antifungal, antibacterial and antihelmintic properties. It causes membrane damage to *Pythium* spp. and also displayed inhibitory effects to its zoospores. Pyrrolnitrin inhibits fungal respiratory chains. HCN is released as product of secondary metabolism by several microorganisms and affects sensitive organisms by inhibiting the synthesis of ATP-mediated cytochrome oxidase. Studies have shown the role of HCN produced by many rhizospheric bacteria in disease suppression of the pathogens. Various bacterial genera have been reported for HCN production, including species of *Alcaligenes*, *Aeromonas*, *Bacillus*, *Pseudomonas* and *Rhizobium*. *Bacillus* spp. produces various biotics, such as polymyxin, circulin and colistin, which are active against Gram-positive and Gram-negative bacteria, as well as an many pathogenic fungi. The growth and development of filamentous fungi can be repressed both *in vitro* and *in vivo* by lytic enzymes, such as chitinases and gluconases produced by *Bacillus* and *Pseudomonas* spp. (Maksimov et al., 2011). *Bacillus* species can exert biocontrol which is being characterized at the molecular level. The biosynthetic gene cluster responsible for the production of the antibiotic zwittermycinA in *Bacillus cereus* has been identified (Milner et al., 1999). *Pseudomonas* produces thiamine which acts as an important factor in quorum sensing dependent expression of biological control. Global regulation and quorum sensing are key factors involved in the biosynthesis of most anti-fungal metabolites anti-fungal metabolites (AFMs). The *gacS/gacA* gene directs global regulation which encodes a two-component regulatory system that senses an unknown signal(s). However, in quorum sensing involved by an Acyl-Homoserine Lactone (AHL) synthase, such as LuxI v leads to the production of *N*-acyl homoserine lactone (AHL) signal molecules. The AHL causes activation of a transcriptional regulator, such as LuxR which then stimulates gene expression (Bloemberg and Lugtenberg, 2001).

Induced systemic resistance (ISR) has been reported as one of the mechanisms by which PGPR reduces plant disease, through the manipulation of the host plant's physical and biochemical properties. Interaction of rhizobacteria with plant roots results in enhancement of plants defensive capacity against a broad spectrum of pathogens and pests, phenomenon called ISR (Lugtenberg and Kamilova, 2009). ISR involves jasmonic acid (JA) and ethylene (ET) signaling pathways within the plant and these hormones stimulate the host plant's defense responses against a variety of plant pathogens (Glick, 2012). Pieterse et al. (1998) reported that ISR triggered by *Pseudomonas fluorescens* WCS417r signals resistance responses through JA and ET dependent pathways. A regulator protein NPR1 is required for expression of ISR. Jetiyanov and Kloepper (2002) observed that PGPR mediate biological control indirectly by eliciting ISR against a number of plant diseases. Rhizobacterial elicited ISR has been demonstrated in many

plant species, including *Arabidopsis*, carnation, cucumber, radish, tobacco and tomato (Van Loon et al., 2007). One of the consequences of ISR reported is the reinforcement of the cell wall through enhanced lignin synthesis and callose apposition. The bacterial components known to induce ISR are lipopolysaccharides (LPS), flagella, siderophores, cyclic lipopeptides, 2,4-diacetylphloroglucinol, homoserine lactones, and volatiles like, acetoin and 2,3-butanediol (Lugtenberg and Kamilova 2009). A large number of defense enzymes that have been associated with ISR include phenylalanine ammonia lyase (PAL), chitinase, β -1,3-glucanase, peroxidase (PO), polyphenol oxidase (PPO), superoxide dismutase (SOD), catalase (CAT), lipoxygenase (LOX), ascorbate peroxidase (APX) and proteinase inhibitors. These enzymes cause release of molecules that elicit the initial steps in induction of resistance (Van Loon et al., 2007).

6. STRESS ALLEVIATION

Rhizobacteria can provide protection to plants against the deleterious effects of environmental stresses, such as drought, flooding, high temperature and salinity. Different mechanisms are exhibited by rhizobacterial strains imparting resistance to plants against various stresses. The term induced systemic tolerance (IST) has been proposed for rhizobacterial induced physical and chemical changes that result in enhanced tolerance to abiotic stress (Yang et al., 2009). One of the mechanisms employed by rhizobacterial strains ensuring plant survival under stressed conditions involves the modification in content of bacterial phytohormones, such as auxins, gibberellins, cytokinins and ABA (Bresson et al., 2013). Production of IAA, gibberellins by PGPR strains displayed increased root length, root surface area and number of root tips, causing enhanced nutrient uptake thus improving plant growth under stress conditions (Egamberdieva and Kucharova, 2009). Drought and salinity disrupt photosynthesis and increases photorespiration, causing enhanced production of reactive oxygen species (ROS), such as the superoxide radical, hydrogen peroxide and hydroxyl radical. Excess ROS causes damages to proteins, DNA and lipids, so it is mandatory to regulate the ROS levels through the coordination of ROS production and ROS scavenging systems to combat oxidative damage occurring during stress conditions. A significant relation between drought stress and antioxidant enzyme activity has been reported. Inoculating maize plants with *Bacillus* species imparted protection against drought stress by reduced activity of antioxidant enzymes APX and Glutathione peroxidase (GPX) (Vardharajula et al., 2011). Rhizobacterial strains possess the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase which cleaves the plant ethylene precursor ACC to ammonia and α -ketobutyrate, thereby causing reduced ethylene level during stressed conditions. Bacterial ACC deaminase confers tolerance against water deficit in tomato and pepper plants inoculated with *Achromobacter piechaudii* ARV8 (Mayak et al., 2004). Siddikee et al. (2010) reported that inoculation with 14 halotolerant bacterial strains ameliorated salt stress in canola plants through the reduction of ethylene production via ACC deaminase activity.

Rhizobacterial production of osmoprotectants such as sugars and amino acids is another acclimatization response observed under stressed conditions. Proline synthesis

has been shown to be increased in abiotically stressed plants in the presence of beneficial bacteria, such as *Burkholderia*, as well as *Arthrobacter* and *Bacillus* (Sziderics et al., 2007). Plants treated with exopolysaccharide (EPS) producing bacteria showed resistance to water stress through improved soil structure and soil aggregation (Sandhya et al., 2009). EPS binds Na^+ ions which decrease its accumulation in plants and preventing their transfer to leaves thus alleviating salt stress in plants (Ashraf et al., 2004). *Bacillus subtilis* produces volatile organic compounds resulting in decreased expression of high-affinity K^+ transporter (*HKT1*) in roots, but its upregulation in the shoots, thus decreasing root Na^+ import, but facilitating Na^+ exclusion from the shoot by retrieving Na^+ from the xylem and facilitating root-to-root Na^+ recirculation (Zhang et al., 2008). Production of heat shock proteins (Berjak, 2006), dehydrins (Timmusk and Wagner, 1999) and volatile organic compounds (Ryu, 2004) have also been reported to impart tolerance to plants against abiotic stresses.

Production of volatile organic compounds (VOCs) by rhizobacteria show antimicrobial and plant-growth modulating activities. VOCs promote plant growth by regulating auxin homeostasis in which the gene expression for auxin production was upregulated. In addition, microarray data revealed coordinated regulation of cell wall loosening enzymes that implicated cell expansion with *B. subtilis* GB03 exposure (Zhang et al., 2007). *Bacillus subtilis* and *B. amyloliquefaciens* produced 3-hydroxy-2-butanone and 2,3-butanediol which enhanced total leaf surface area and induced systemic resistance (ISR) of *A. thaliana* (Ryu et al., 2004).

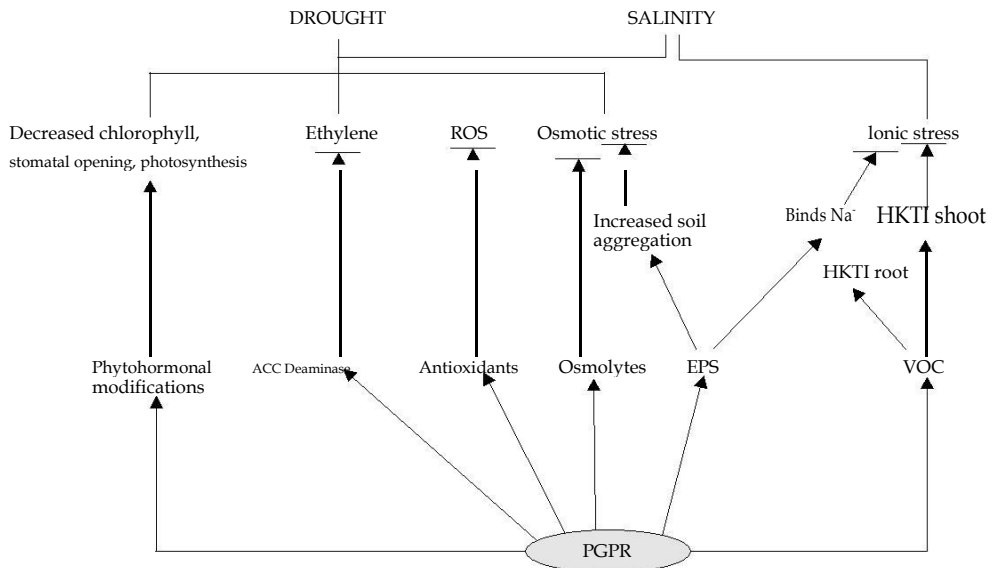


Fig. 3.2 Stress alleviating mechanisms of rhizobacteria

(Abbreviations: ROS, reactive oxygen species; *HKT1*, high affinity K^+ transporter; ACC, 1-aminocyclopropane-1-carboxylate; VOC, volatile organic compound; EPS, exopolysaccharides)

7. CONCLUSION

Rhizobacteria are efficient microbial competitors in the root zone to enhance plant growth directly through biofertilization, phytostimulation and indirectly by reducing soil-borne pathogens. The application of rhizobacteria to crops as inoculants is a trend for future as it substantially reduces the chemical inputs thus contributing towards increased crop yields. In addition, various rhizobacterial strains imparting stress tolerance have been identified. However, there is need to develop more effective and longer shelf-lived PGPR strains to achieve sustainable crop production in agroecosystems.

Acknowledgements

The author is thankful to ICRISAT and ICAR for supporting research work done.

References

- Ahmad F, Ahmadand I, and Khan MS (2008). Screening of free living rhizospheric bacteria for their multiple plant growth promoting activities. *Microbiol Res* 163(2):173–181.
- Alcazar R, Bitrian M, Bartels D, Koncz C, Altabella T, and Tiburcio AF (2010). Polyamines, molecules with regulatory functions in plant abiotic stress tolerance. *Planta* 231:1237–1249.
- Anith KN, Momol MT, Kloepper JW, Marois JJ, Olson SM, and Jones JB (2004). Efficacy of plant growth promoting rhizobacteria, acibenzolar-S-methyl and soil amendment for integrated management of bacterial wilt of tomato. *Plant Disease* 88: 669–673.
- Arkhipova TN, PrinsenE, Veselov SU, Martinenko EV, Melentiev AI, and Kudoyarova GR (2007). Cytokinin producing bacteria enhance plant growth in drying soil. *Plant and Soil* 292: 305–315.
- Ashraf M, Berge SH, and Mahmood OT (2004). Inoculating wheat seedling with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. *Biol Fert Soils* 40:157–162.
- Berjak P (2006). Unifying perspectives of some mechanisms basic to desiccation tolerance across life forms. *Seed Sci Res* 16: 1–15.
- Bhattacharyya PN, and Jha DK (2012). Plant growth-promoting rhizobacteria (PGPR): emergence in agriculture. *World J Microbiol Biotechnol* 28: 1327–1350.
- Bloemberg GV, and Lugtenberg BJ (2001). Molecular basis of plant growth promotion and biocontrol by rhizobacteria. *Curr Opin Plant Biol* 4: 343–350.
- Bresson J, Varoquaux F, Bontpart T, Touraine B, and Vile D (2013). The PGPR strain *Phyllobacterium brassicacearum* STM196 induces a reproductive delay and physiological changes that result in improved drought tolerance in *Arabidopsis*. *New Phytol* 200: 558–569.

- Cantero EV, Calderon EH, Becerra CV, Meza JE, Lopez M, Cuevas RA, and Bucio JL (2007). Role of dissimilatory fermentative iron-reducing bacteria in Fe uptake by common bean (*Phaseolus vulgaris* L.) plants grown in alkaline soil. *Plant Soil* 291: 263–273.
- Cassan F, Maiale S, Masciarelli O, Vidal A, Luna V, and Ruiz O (2009). Cadaverine production by *Azospirillum brasilense* and its possible role in plant growth promotion and osmotic stress mitigation. *Eur J Soil Biol* 45: 12–19.
- Cattelan AJ, Hartel PG, and Fuhrmann JJ (1999). Screening of plant growth promoting rhizobacteria to promote early soybean growth. *Soil Sci Soc Am J* 63: 1670–1680.
- Chakraborty U, Chakraborty B, and Basnet M (2006). Plant growth promotion and induction of resistance in *Camellia sinensis* by *Bacillus megaterium*. *J Basic Microbiol* 34: 925–929.
- Dodd IC, Zinovkina NY, Safronova VI, and Belimov AA (2010). Rhizobacterial mediation of plant hormone status. *Annal Appl Biol* 157: 361–379.
- Duijff BJ, Bakker PAHM, and Schippers B (1994). Suppression of *Fusarium* wilt of carnation by *Pseudomonas putida* WCS358 at different levels of disease incidence and iron availability. *Biocontrol Sci Techn* 4: 279–288.
- Egamberdieva D, and Kucharova Z (2009). Selection for root colonizing bacteria stimulating wheat growth in saline soils. *Biol Fert Soil* 45: 561–573.
- Fulchieri M, Lucangeli C, and Bottini R (1993). Inoculation with *Azospirillum lipoferum* affects growth and gibberellin status on corn seedling roots. *Plant Cell Physiol* 34: 1305–1309.
- Glick BR (2012). Plant growth-promoting bacteria: mechanisms and applications. *Scientifica*. Article ID 963401, 15 pages, <http://dx.doi.org/10.6064/2012/963401>.
- Gray EJ, and Smith DL (2005). Intracellular and extracellular PGPR: commonalities and distinctions in the plant–bacterium signalling processes. *Soil Biol Biochem* 37:395–412.
- Guo JH, Qi HY, and Li SM (2002). Biocontrol efficiency of three PGPR strains admixture of pepper bacterial wilt. *Bacterial Wilt Newsletter* 17:3.
- Islam MR, Ahamed R, Rahman MO, Akbar MA, Al-Amin M, Alam KD, and Lyzu F (2010). In vitro antimicrobial activities of four medicinally important plants in Bangladesh. *Eur J Sci Res* 39: 199–206.
- Jetiyanov J, and Kloepper JW (2002). Mixture of plant growth promoting rhizobacterial for induction of systemic resistance against multiple plant diseases. *Biol Control* 24: 285–291.
- Kaushal M, and Kaushal R (2013). Screening and characterization of plant growth promoting rhizobacteria isolated from rhizosphere of cauliflower (*Brassica oleracea* var. *botrytis* L.). *Afr J Microbiol Res* 7(17): 1657–1663.

- Leeman M, Van Peet JA, Den Quden FM, Henisbroek M, Bakker PAHM, and Schippers B (1996). Iron availability affects induction of systemic resistance to *Fusarium* wilt of radish by *Pseudomonas fluorescens*. *Phytopathol* 86: 149–155.
- Lugtenberg B, and Kamilova F (2009). Plant growth promoting rhizobacteria. *Annu Rev Microbiol* 63: 541–556.
- Maksimov IV, Abizgil'dina RR, and Pusenkova LI (2011). Plant growth promoting rhizobacteria as alternative to chemical crop protectors from pathogens (Review). *Appl Biochem Microbiol* 47: 333–345.
- Mantelin S, and Touraine B (2004). Plant growth-promoting rhizobacteria and nitrate availability: impacts on root development and nitrate uptake. *J Expt Bot* 55: 27–34.
- Mariano RLR, Luna CL, and Souto Maior AM (2002). Production of biocontrol agent for crucifers black rot disease. *Braz J Chem Eng* 19(2): 133–140.
- Mayak S, Tirosh T, and Glick BR (2004). Plant growth promoting bacteria that confer resistance to water stress in tomato and pepper. *Plant Sci* 166: 525–530.
- Milner JL, Stohl EA, and Handelsman J (1999). Zwittermicin A biosynthetic cluster. *Gene* 237: 403–411.
- Molina-Favero C, Creus CM, Simontacchi M, Puntarulo S, and Lamattina L (2008). Aerobic nitric oxide production by *Azospirillum brasilense* Sp245 and its influence on root architecture in tomato. *Mol Plant Microbe Interact* 21: 1001–1009.
- Paul D, and Sharma YR (2006). Plant growth promoting rhizobacteria (PGPR)-mediated root proliferation in black pepper (*Piper nigrum* L.) as evidenced through GS Root software. *Arch Phytopathol Plant Protect* 39: 1–4.
- Perrig D, Boiero ML, Masciarelli OA, Penna C, Ruiz OA, Cassan FD, and Luna MV (2007). Plant-growth-promoting compounds produced by two agronomically important strains of *Azospirillum brasilense*, and implications for inoculant formulation. *Appl Microbiol Biotechnol* 75: 1143–1150.
- Pieterse CMJ, Van Wees SCM, Van Pelt JA, Knoester M, Laan R, Gerrits H, Weisbeek PJ, and Van Loon LC (1998). A novel signaling pathway controlling induced systemic resistance in Arabidopsis. *Plant Cell* 10: 1571–1580.
- Prasad R, Garg AP, and Varma A (2005). Interaction of medicinal plants with plant growth promoting rhizobacteria and symbiotic fungi. In: Podila GK, Varma A (eds), *Basic Research and Applications of Mycorrhizae*. IK International Pvt Ltd. New Delhi, India, 1: 363–40719.
- Prasad R, Kumar V, and Prasad KS (2014). Nanotechnology in sustainable agriculture: present concerns and future aspects. *African Journal of Biotechnology* 13(6): 705–713.
- Prasad R, Kumar M, and Varma A (2015). Role of PGPR in soil fertility and plant health. In: Egamberdieva D, Shrivastava S, Varma A (eds) *Plant Growth-Promoting Rhizobacteria and Medicinal Plants*, Springer International Publishing Switzerland 247–260.

- Recep K, Fikretin S, Erkol D, and Cafer E (2009). Biological control of the potato dry rot caused by *Fusarium* species using PGPR strains. *Biol Control* 50(2):194-198.
- Rodrigues EP, Rodrigues LS, de Oliveira ALM, Baldani VLD, Teixeira KR, Urquiaga S, and Reis VM (2008). *Azospirillum amazonense* inoculation: Effects on growth, yield and N₂-fixation of rice (*Oryza sativa* L.). *Plant Soil* 302: 249-261.
- Ryu CM (2004). Bacterial volatiles induce systemic resistance in *Arabidopsis*. *Plant Physiol* 134: 1017-1026.
- Ryu CM, Farag MA, Hu CH, Reddy MS, Kloepper JW, and Pare PW (2004). Bacterial volatiles induce systemic resistance in *Arabidopsis*. *Plant Physiol* 134: 1017-1026.
- Sandhya V, Ali SkZ, Grover M, Reddy G, and Venkateswarlu B (2009). Alleviation of drought stress effects in sunflower seedlings by exopolysaccharides producing *Pseudomonas putida* strain P45. *Biol Fert Soil* 46: 17-26.
- Sharma A, Johri BN, Sharma AK, and Glick BR (2003). Plant growth promoting bacterium *Pseudomonas* spp. strain GRP3 influences iron acquisition in mung bean (*Vigna radiate* L. Wilzeck). *Soil Biol Biochem* 35: 887-894.
- Siddikee MA, Chauhan PS, Anandham R, Han GH, and Sa T (2010). Isolation, characterization, and use for plant growth promotion under salt stress, of ACC deaminase - producing halotolerant bacteria derived from coastal soil. *J Microbiol Biotechnol* 20: 1577-1584.
- Srivastav S, Yadav KS, and Kundu BS (2004). Prospects of using phosphate solubilizing *Pseudomonas* as biofungicide. *Ind J Microbiol* 44: 91-94.
- Sziderics AH, Rasche F, Trognitz F, Sessitsch A, and Wilhelm E (2007). Bacterial endophytes contribute to abiotic stress adaptation in pepper plants (*Capsicum annuum* L.). *Can J Microbiol* 53: 1195-1202.
- Timmusk S, Wagner EGH (1999). The plant growth-promoting rhizobacterium *Paenibacillus polymyxa* induces changes in *Arabidopsis thaliana* gene expression: a possible connection between biotic and abiotic stress responses. *Mol Plant Microbe Inter* 12: 951-959.
- Van Loon LC (2007). Plant responses to plant growth-promoting rhizobacteria. *Eur J Plant Pathol* 119: 243-254.
- Vardharajula S, Zulfikar Ali S, Grover M, Reddy G, and Bandi V (2011). Drought-tolerant plant growth promoting *Bacillus* sp. effect on growth, osmolytes and antioxidant status of maize under drought stress. *J Plant Inter* 6: 1-14.
- Yang J, and Kloepper JW, Ryu CM (2009). Rhizosphere bacteria help plants tolerate abiotic stress. *Trends Plant Sci* 14: 1-4.
- Zhang H, Kim MS, Krishnamachari V, Payton P, Sun Y, Grimson M, Farag MA, Ryu CM, Allen R, Melo IS, and Pare PW (2007). Rhizobacterial volatile emissions regulate auxin homeostasis and cell expansion in *Arabidopsis*. *Planta* 226: 839-851.
- Zhang H, Kim MS, Sun Y, Dowd SE, Shi H, and Pare PW (2008). Soil bacteria confer plant salt tolerance by tissue-specific regulation of sodium transporter HKT1. *Mol Plant Microbe Interact* 21: 737-744.