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Poonam Gusain
Regional Science Center, Uttarakhand State Council for Science and Technology, Dehradun, Uttarakhand, India

BS Bhandari
Department of Botany & Microbiology, HNB Garhwal University Srinagar, Garhwal, Uttarakhand, India

Correspondence
Poonam Gusain
Regional Science Center, Uttarakhand State Council for Science and Technology, Dehradun, India

Rhizosphere associated PGPR functioning

Poonam Gusain and BS Bhandari

Abstract
Sustainability of agricultural production is very important to fulfill the growing demands of food to feed the world increasing population. Use of plant growth-promoting rhizobacteria (PGPR) as efficient biofertilizer seems an ideal tool to mitigate global dependence on hazardous agrichemicals and improve food security. The microbial population colonizing rhizosphere includes bacteria, fungi, actinomycetes, protozoa, and algae. Free-living bacteria associated with rhizosphere, beneficial to plant growth, usually include the cyanobacteria of the genera *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium, Rhizobium, and Sinorhizobium.* Free-living nitrogen fixing bacteria or associative nitrogen fixers belonging to the species *Azospirillum, Enterobacter, Klebsiella* and *Pseudomonas*, have been shown to attach to the root and efficiently colonize root surfaces. Generally, plant growth promotion and development can be facilitated in various ways: preventing of the deleterious effects of phytopathogens by synthesizing biogenic chelator compounds such as siderophores, facilitating the production of plant hormones such as auxins, cytokinins, gibberellins, ethylene, antibiotics, volatile metabolites, enzymes, abscisic acid, and solubilization of mineral phosphates and other nutrients have been reported for several PGPR bacterial genera. Hence, this review highlights the key mechanisms employed by PGPR bacteria to facilitate plant growth to increase the health and productivity of cultivated soils.

Keywords: Rhizosphere, PGPR, rhizoremediation, PGPR traits, agriculture sustainability

Introduction
The rhizosphere is most dynamic habitats on the earth, and major driving force to ecosystem functioning and diversity. The dynamic interactions between rhizodeposits, microbial communities are major factors shaping rhizosphere world. Root exudation plays a pivotal role in determining the rhizosphere population. Root exudation includes a diverse array of chemical compounds secreted by roots, ranging from the secretion of ions, free oxygen, water, enzymes, mucilage, carbon-containing primary and secondary metabolites, numerous aromatic compounds (i.e. terpernes, flavonoids or lignin-derived components) and actively metabolizing soil microbial communities. Plants exert beneficial, neutral and harmful effects from intimacy with microbial partners. Rhizosphere microorganisms such as bacteria, fungi, nematodes, protozoa, algae and microarthropods also have a crucial role in complex food web that utilizes the large amount of carbon that is fixed by the plant and released into the rhizosphere. Root exudation plays a crucial role in determining the symbiotic and protective associations between plant and soil microorganisms. Acidification of the rhizosphere lowers the status of major macronutrients such as manganese, iron and aluminum resulting in phytotoxic effects on plant roots and beneficial microbes. Deleterious microorganisms present in the rhizosphere are presumed to adversely affect plant growth and development through the production of toxic metabolites *viz*., rhizobitoxine, produced by *Bradyrhizobium* strains, gabaculin a product of *Streptomyces toyacaenis*, gostatin a product of *Streptomyces sumanensis*, thiolactomycin produced by several species of *Norcardia* and *Streptomyces* are well documented potent phytotoxins (Table 1). Rhizosphere also harbors more than 8,000 species of fungi, living symbiotically or causing diseases in plants were described in the literature, for example *Agrobacterium tumefaciens*, the causal agent of crown gall. *Rhizoctonia solani* is most common pathogen primarily causing soilborne fungal disease in soybean. Soilborne fungal pathogens that mostly involved in agricultural crop loss are *Fusarium*, *Phytophthora*, *Pythium*, and *Rhizoctonia* (Trabelsi and Mhamdi 2013; Saraf *et al*. 2014; Susilowati *et al*. 2011) [94, 83, 91].

Table 1: Reported pathogenic microorganisms affect plant health and growth by different mechanisms of action

Microorganisms	Strain	Target plant	Observed effects	Reference
Chromobacterium violaceum	CV0	*Arabidopsis thaliana*	Growth inhibition	Blom *et al*., (2011a) [14]
Pseudomonas aeruginosa	PAO1, PAO14, TB, TBCF10839, PUPa3	*A. thaliana*	Growth inhibition	Blom *et al*., (2011a) [14]; Rudrappa *et al*., (2010) [80]
Pseudomonas fluorescens	A112	*T. aestivum*	Reduction of shoot length, root length and root numbers	Astrom and Gerhardson (1989) [8]
Pseudomonas fluorescens	CHAO, L13–6-12	*A. thaliana*	Growth inhibition	Blom *et al*., (2011a) [14]; Rudrappa *et al*., (2010) [80]; Vespermann Kai and Piechulla (2007) [95]
Pseudomonas trivialis	3Re2–7	*A. thaliana*	Growth inhibition	Vespermann *et al*., (2007) [95]
Serratia marcescens	MG-1	*A. thaliana*	Growth inhibition	Blom *et al*., (2011a) [14]
Serratia odorifera	4Rx13	*A. thaliana*	Growth inhibition	Vespermann *et al*., (2007) [95]
Serratia plymuthica	3Re4–18	*A. thaliana*	Growth inhibition	Vespermann *et al*., (2007) [95]
Serratia plymuthica	HRO-C48	*A. thaliana*	Growth inhibition	Vespermann *et al*.,(2007) [95]
Serratia plymuthica	IC14	*A. thaliana*	Growth inhibition	Blom *et al*., (2011a) [14]
Stenotrophomonas rhizophila	P69	*A. thaliana*	Growth inhibition	Vespermann *et al*., (2007) [95]
Stenotrophomonas maltophilia	R3089	*A. thaliana*	Growth inhibition	Vespermann *et al*., (2007) [95]
Burkholderia strains		*A. thaliana*	Strain and medium dependent growth promotion and inhibition	Blom *et al*., (2011b) [15]
Serratia marcescens	MG-1	Fungi and plants	Growth inhibition	Vespermann *et al*., (2007) [95]
Stenotrophomanas maltophilia	R3089	Fungi and plants	Growth inhibition	Vespermann *et al*., (2007) [95]
Stenotrophomanas rhizospehila	P69	Fungi and plants	Growth inhibition	Vespermann *et al*., (2007) [95]
Muscodor yucatanensis		Fungi and plants	Allelochemical effects against other endophytic fungi, and phytopathogenic	Saraf, Pandya and Thakkar (2014) [83]
S. viridochromogenes		Plants	Growth inhibition	Barazani and Friedman (2001) [9]
S. hygroscopicus		Plants	Growth inhibition	Barazani and Friedman (2001) [9]

The fast industrialization all around the world leads to unfortunate consequences such as, the production and release of considerable amounts of toxic wastes to the environment. Additionally, microbes have evolved several mechanisms to make toxic metals more bioavailable to plants, comprising transformation, reduction, oxidation and chelation and metabolism of organic-metal complexes that results in the release of metals (Nie *et al*. 2002; Dell-Amico *et al*. 2008) [66, 23]. Rhizoremediation properties of plants and plant growth promoting rhizobacteria for the removal of hazardous compounds like toxic metals and organic pollutants is extensively studied by various researchers. Some organic contaminants defined as; total petroleum hydrocarbons (TPHs) and polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) can persist in the environment for a long time and pose great threat to human health. The biological methods for the cleanup of hazardous compounds present in the environment have obvious advantages due to several reasons; cost-effectiveness, convenient and complete degradation of organic pollutants, and no collateral destruction of the site material or indigenous flora and fauna (Zhuang *et al*. 2007; Lucy *et al*. 2004; Gianfreda and Rao 2004) [101, 52, 29]. The combination of PGPR and hyper accumulator plants was found to be effective against organic pollutants and heavy metals (Table 2).

Table 2: Summary of plant growth promoting rhizobacteria tested for various contaminants including heavy metals and organic pollutants on different crop plants

Rhizospher microbes	Plant	Contaminant	Role of PGPR	Reference
Azospirillum lipoferum strain 15	Wheat	Crude oil	Development of wheat root system	Muratova *et al*., (2008) [62]
Azospirillum brasilense Cd	Tall fescue	Polycyclic aromatic hydrocarbons (PAHs)	Increased plant tolerance to PAHs	Huang *et al*., (2004) [40]
Enterobactor cloacae CAL2	Tall fescue	Total petroleum hydrocarbons (TPHs)	Promoted plant growth	Huang *et al*., (2004) [40]
Pseudomonas fluorescens F113	Alfalfa			
Pseudomonas putida Flav1-1	Arabidopsis	Polychlorinated biphenyls (PCBs)	More effectively degraded PCBs with bph gene cloned	Villacieros *et al*., (2005) [96]
Dietzia maris	Wheat	Cd	Promoted plant growth	Gusain *et al*., 2017 [37]
Lysinibacillus sp	Wheat	Cd	Promoted plant growth	Gusain *et al*., 2017 [37]
Pseudomonas sp.	Arabidopsis	Polychlorinated biphenyls(PCBs)	Utilized plant secondary metabolites	Narasimhan *et al*., (2003) [64]
Pseudomonas aeruginosa strain OSG41	Chickpea	Cr	Growth promotion	Oves *et al*., (2013) [69]
Acinetobacter haemolyticus RP19	Pearl millet	Zn	Increased significantly root length, shoot length and biomass	Misra *et al*., (2012) [60]

Pseudomonas sp. A3R3	Indian mustard	Ni	Increased significantly root length, shoot length and biomass	Ma *et al*. (2011) [55]
Pseudomonas sp. TLC 6-6.5-4	Zea mays,	Cu	Increased significantly root length, shoot length and biomass	Li and Ramakrishna (2011) [51]
Enterobacter aerogenes NBRI K24, *Rahnella aquatilis* NBRI K3	Indian mustard	Ni, Cr	Growth promotion	Kumar *et al*. (2009)
Pseudomonas aeruginosa strain MKRh3	Black gram	Cd	Growth promotion	Ganesan (2008) [28]
Burkholderia sp. J62	Tomato	Pb, Cd	Growth promotion	Jiang *et al*. (2008) [42]
Pseudomonas fluorescens	Soybean	Hg	Growth promotion	Gupta *et al*. (2005) [36]
Enterobacter cloacae UW41	Canola	As	Increased biomass and metal accumulation	Nie *et al*.(2002) [66]

Plant growth promoting rhizobacteria: The multifactorial below ground network

The term "plant-growth-promoting-rhizobacteria" has been coined to encompass bacteria, inhabiting plant roots and influencing the plant growth positively by diverse mechanisms. PGPR, that can enhance plant growth and protect plants from disease, classified in two mazor groups, based on the degree of bacterial proximity to root intimacy (Gray and Smith 2005) (Figure 1) [35].

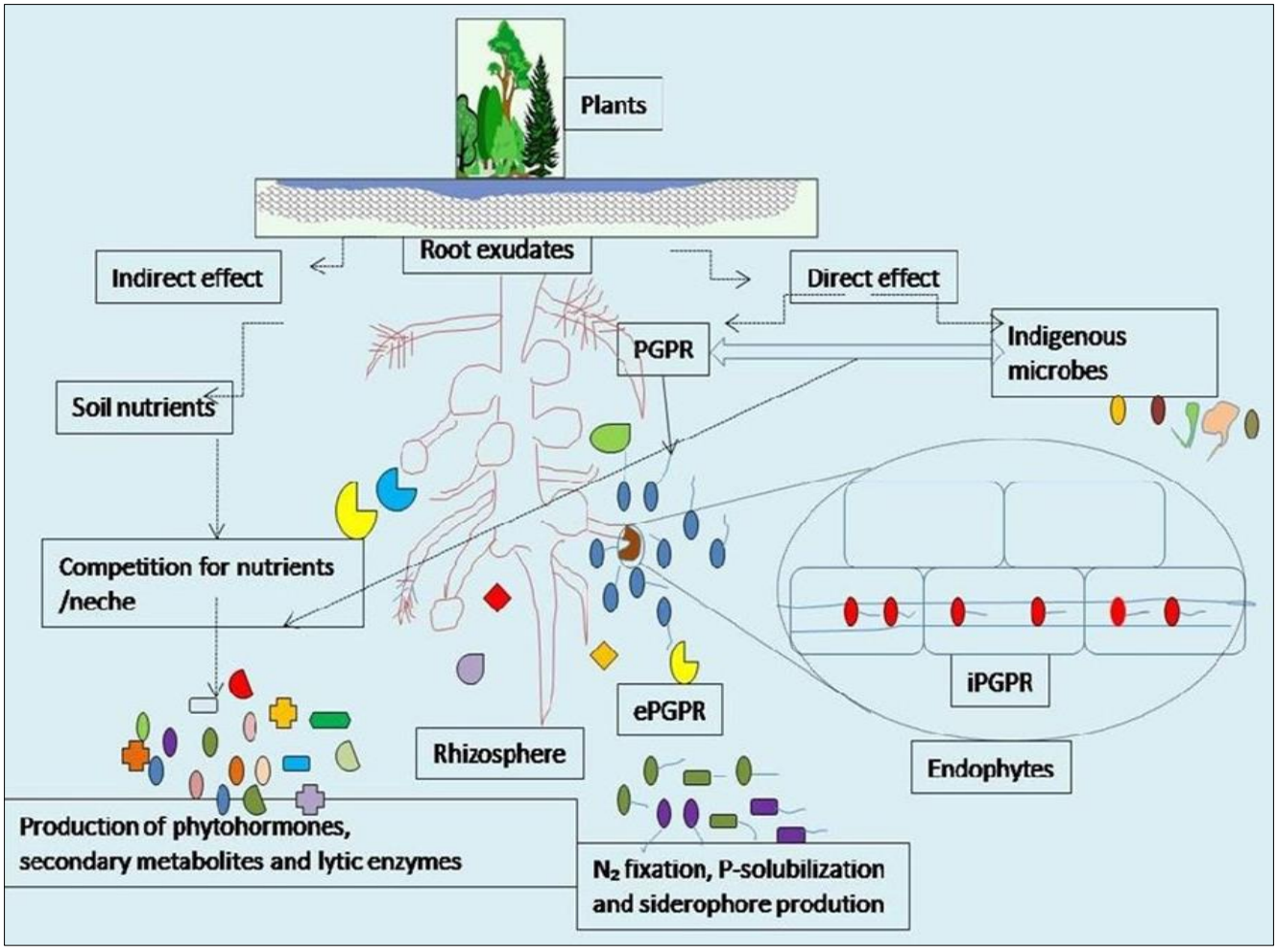

Fig 1: The figure showing root exudation exerts direct effect to maintain proximity with microbial partners. Indirectly soil nutrients and rhizosphere deposits also attract microbial community to compete for the substances and niche to grow. In figure intracellular plant growth promoting rhizobacteria (iPGPR) those colonizing root interior and forming nodular structures, are illustrated in red color. Several extracellular plant growth promoting rhizobacteria (ePGPR) colonize around the plant roots in rhizosphere

PGPR enter the root interior to establish endophytic populations in specialized nodular structures with adaptability to the niche and benefits to the host plants are defined as intracellular plant growth promoting rhizobacteria (iPGPR). *Bradyrhizobium, Mesorhizobium, Allorhizobium, Azorhizobium and Rhizobium* are examples of iPGPR. However extracellular plant growth promoting rhizobacteria (ePGPR) colonize around the plant roots in rhizosphere, are *Chromo bacterium, Pseudomonas, Serratia, Erwinia, Agrobacterium, Arthrobacter, Caulobacter, Flavobacterium, Azotobacter, Azospirillum, Bacillus, Burkholderia*, and *Micrococcous* (Compant *et al*. 2005; Bhattacharyya and Jha 2012) [19, 12].

Functional diversity of plant growth promoting rhizobacteria is characterized as (i) biofertilizers (increasing the availability of nutrients to plant), (ii) phytostimulators (plant growth promotion, generally through phytohormones), (iii) rhizoremediators (degrading organic pollutants) and (iv) biopesticides (controlling diseases, mainly by the production of antibiotics. Root associated rhizobacteria are more versatile in transforming, mobilizing, solubilizing the nutrients compared to those from bulk soils (Kloepper *et al*. 2004;

Somers *et al*. 2004; Legtenberg and Kamilova 2009; Hayat *et al*. 2010) [45, 87, 53, 38].

Plants have gained enormous advantages from mutual association with plant growth promoting microbes, for example the delivery of fixed nitrogen, resource acquisition (phosphorus and essential minerals), modulating the level of phytohormones referred as gibberellins, cytokinins, abscisic acid, and auxins, production of metabolities such as hydrogen cyanide (HCN), 2, 4- diacetylphloroglucinol (DAPG), antibiotics, e.g., phenazine and volatile compounds, are essential for plantgrowth (Duffy *et al*. 2004) [27].

Evidently, PGPR holds enormous prospects in improved and sustainable crop production including reduced use of chemical inputs. The growing cost of fertilizers and demand for pesticide-free food has led to a search for an alternative approach that might alleviate the problem. Interactions between plants and beneficial rhizosphere microorganisms can enhance crop production and tolerance of plants to degraded environment (Ahemad and Kibert 2014; Sayyed and Patel 2011) [84].

Plant growth promoting rhizobacterial tools

A wide range of classical and molecular approaches are applied in progress of identifying uncharacterized new PGPR community, using phenotypic methods that rely on the ability to culture microorganisms include standard plating methods on selective media, community level physiological profiles (CLPP) using the BIOLOG system, phospholipid fatty acid (PLFA), fatty acid methyl ester (FAME) profiling, and nonbiased screening strategies that rely on gene fusion technologies. A variety of bacterial traits and specific genes contribute to root colonization, includes reporter transposons and *in vitro* expression technology (IVET) have been applied to detect diverse PGPR genes expressed during colonization. The plethora of research using molecular markers such as green fluorescent protein (GFP) or fluorescent antibodies are capable of tracking location of individual rhizobacteria on the root using confocal laser scanning microscopy. This approach has also been combined with ribosomal RNA-targeting (rRNA) probe to monitor the metabolic activity of specific rhizobacterial strains, and showed that bacteria located at the root tip were most active (Sorensen *et al*. 2001; Ahmad *et al*. 2011) [88].

Plant growth promoting rhizobacterial traits for plant growth promotion

PGPR microorganisms affect plant fitness through direct or indirect effects on functional traits.

Direct mechanisms occur, when PGPR produce stimulatory metabolites and phytohormones, such as auxins, cytokinins, gibberellins and siderophores (Table 3), the chelating agents that protect plants from diseases (Kamnev and Lelie 2000) [44].

Table 3: Various organic or inorganic substances produced by plant growth promoting rhizobacteria facilitating resource acquisition to stimulate plant growth

PGPR	PGP traits	References
Rahnella aquatilis	ACC deaminase*	Mehnaz, Baig and Lazarovits (2010) [58]
Acinetobacter sp., *Pseudomonas* sp.	ACC deaminase*	Indiragandhi *et al*., (2008) [41]
Enterobacter sp.	ACC deaminase*	Kumar *et al*., (2008)
Burkholderia	ACC deaminase*	Jiang *et al*., (2008) [42]
Pseudomonas jessenii	ACC deaminase	Rajkumar and Freitas (2008) [75]
Pseudomonas aeruginosa	ACC deaminase*	Ganesan (2008) [28]
Achromobacter xylosoxidans A551,	ACC deaminase*	Belimov *et al*., (2005) [10]
Rhizobium hedysari ATCC 43676	ACC deaminase*	Ma *et al*., (2003) [55]
Pseudomonas marginalis DP3	ACC deaminase*	Belimov *et al*., (2005) [10]
Mesorhizobium loti	ACC deaminase*	Sullivan, *et al*., (2002) [90
Rhizobium leguminosarum	Indole-3-acetic acid	Ahemad and Kibret (2014) [3]
Azotobacter sp.	Indole-3-acetic acid	Ahmad *et al*., (2006) [4]
Pseudomonas sp.	Indole-3-acetic acid	Roesti *et al*., (2006) [79]
Bacillus sp, *Paenibacillus* sp.	Indole-3-acetic acid	Beneduzi *et al*., (2008) [11]
Rhizobium leguminosarum b. *Trifolii* ACCC18002	Indole-3-acetic acid	Jin *et al*., (2006) [43]
Streptomyces strains C	Indole-3-acetic acid	Sadeghi *et al*., (2012) [81]
Enterobacter aerogenes NII-0907, *Enterobacter aerogenes* NII-0929, *Enterobacter cloacae* NII-0931, *Enterobacter asburiae* NII-0934	Indole-3-acetic acid	Deepa, *et al*., (2010) [21]
Pseudomonas tolaasii ACC23, *Pseudomonas fluorescens* ACC9, *Alcaligenes* ZN4, *Mycobacterium* sp. ACC14	Indole-3-acetic acid	Dell'Amico *et al*., (2008) [23]
Mesorhizobium loti MP6	Indole-3-acetic acid	Chandra *et al*., (2007) [18]
Enterobacter sp., *Klebsiella*	Indole-3-acetic acid	De Santi Ferrara *et al*., (2013) [24]
Pseudomonas aeruginosa, Pseudomonas fluorescens, Ralstonia metallidurans	Siderophores	Braud *et al*., (2009) [16]
Proteus vulgaris	Siderophores	Rani *et al*., (2009) [74]
Enterobacter sp.	Siderophores	Kumar *et al*., (2008)
Burkholderia	Siderophores	Jiang *et al*., (2008) [42]
Azotobacter sp., *Mesorhizobium* sp.	Siderophores	Ahmad *et al*., (2008) [4]
Mesorhizobium ciceri, Azotobacter chroococcum	Siderophores	Wani *et al*., (2007) [97]
Pseudomonas, Bacillus	Siderophores	Wani *et al*., (2007) [97]
Pseudomonas jessenii	Siderophores	Rajkumar and Freitas (2008) [75]
Bacillus sp. PSB10	Siderophores	Wani *et al*., (2007) [98]
Paenibacillus polymyxa	Siderophores	Ahemad and Kibret (2014) [3]
*Pseudomonas aeruginosa*4EA	Siderophores	Naik and Dubey (2011) [63]
Enterobacter asburiae	Siderophores	Ahemad and Khan (2010)

*Denotes: 1-aminocyclopropane-1-carboxylate (ACC) deaminase

Indirect effects originate when PGPR act like biocontrol agents or stimulate other beneficial symbioses. Here, we review the multifactorial network and underlying mechanisms involved in plant growth promotion conferred by rhizosphere-associated bacteria in order to address the immediate issues characterized as food and nutritional security, climate change and well-being of the planet.

Phytohormone IAA production

Production of the phytohormone, auxin is widespread among plants and root associated bacteria. Microbial synthesis of phytohormones auxins and cytokinins has been reported by various researchers since a long time (Patten and Glick 2002) [71]. Patten and Glick (1996) [70] estimated that 80% of microorganisms isolated from the rhizosphere of various crops possess the ability to synthesize and release auxins as secondary metabolites. According to the conventional classification, the naturally occurring phytohormones are: (i) auxins, (ii) cytokinins, (iii) ethylene, (iv) gibberellins and (v) abscisic acid. The phytohormone auxin is a key regulator of diverse physiological processes in plants including cell division, elongation, differentiation, tropisms, apical dominance, senescence, abscission, seed germination, root formation, branching, tillering, flowering and fruit ripening (Woodward and Bartel 2005; Teale *et al*. 2006) [99, 93]. Moreover four different pathways have been described for the synthesis of IAA from tryptophan in plants and microorganisms despite of some intermediate compounds (Figure 2).

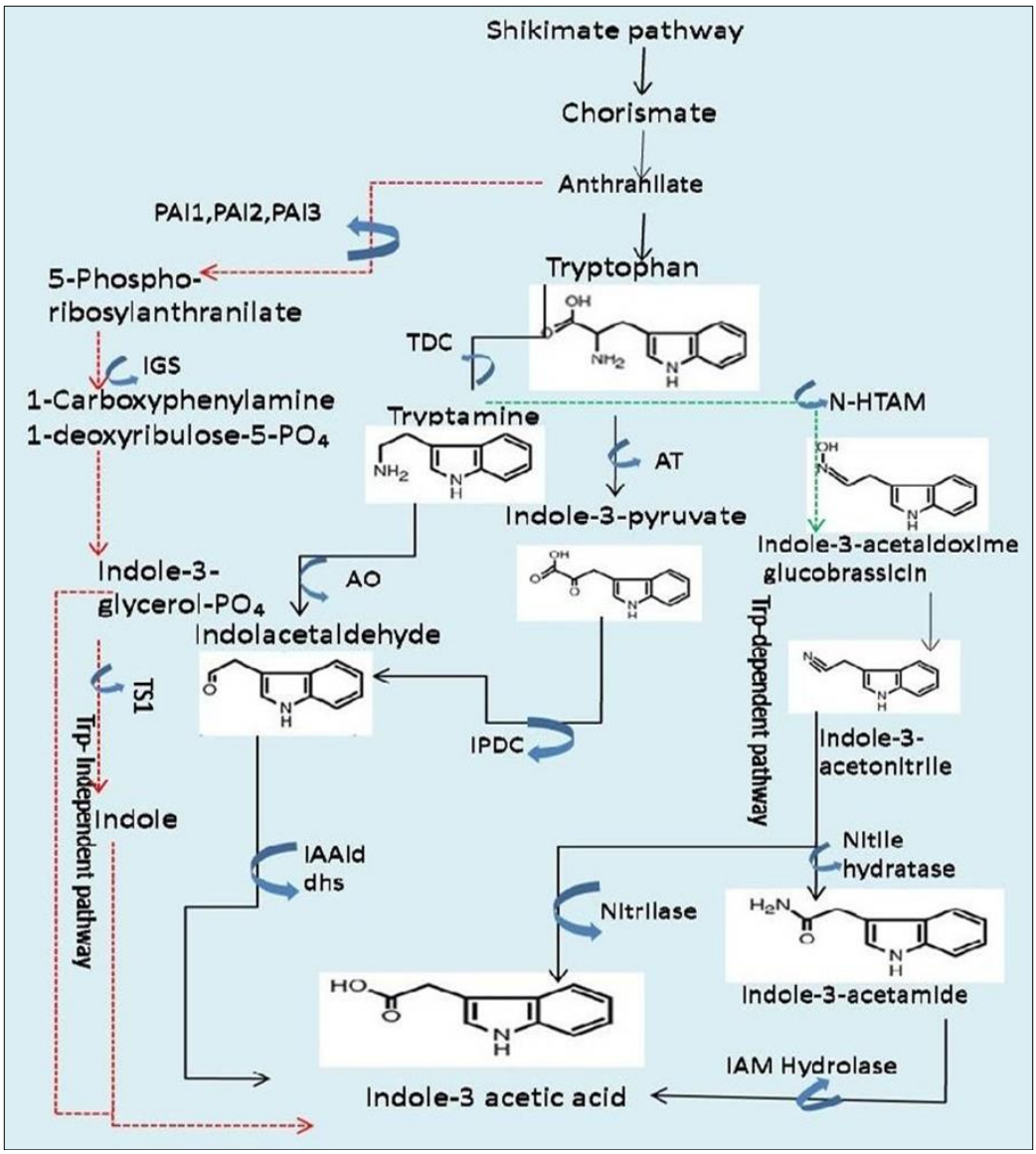

Fig 2: Indole Acetic Acid biosynthetic pathway: The alternative pathway is underlined with a green dashed line, red dashed arrows denote the tryptophan-independent IAA biosynthetic pathway, similarly black lines indicate Trp-dependent IAA synthesis.TSA1; Trp synthase-alpha IGS; indole-3-glycerol phosphate synthase, TS1; Trp synthase-α TDS; Trp decarboxylase, N-HTAM, AT; Amino transferase, AO; Amino-oxidase, IPDC; Indole-3 pyruvate decarboxylase, IAAld; Indole-3-acetaldehyde

In plants, *de novo* synthesis of auxins involve deamination or decaroxylation. (i) Indole Acetic Acid is produced from tryptophan via the intermediate indole acetamide is reported for several phytopathogenic bacteria genera belonging to, *Agrobacterium tumefaciens, Erwinia herbicola* and pathovars of *Pseudomonas syringae* implicated in the induction of plant tumors. (ii) *Bradyrhizobium, Rhizobium, Azospirillum, Klebsiella, Enterobacter* and several other plant growth promoting bacteria synthesize IAA predominantly by alternate tryptophan-dependant pathway, through indole pyruvic acid. (iii) The conversion of indole-3-acetic aldehyde from tryptophan involves an alternative pathway and an

intermediate tryptamine is formed. (iv) The another way of IAA biosynthesis that involves tryptophan conversion into indole-3-acetonitrile is found in most of *Cyanobacteria* sp.

In Trp-independent IAA biosynthesis, indole-3-glycerol phosphate and indole are the likely precursors, although key enzyme encodes in this pathway is indole-3-glycerol phosphate synthase (IGS), which catalyses the conversion of 1-(O-carboxyphenylamino)-1-deoxyribulose-5-phosphate to indole-3-glycerol phosphate. Reports by Asghar *et al*. (2002) showed that PGPR strains produced 24.6 μgml^{-1} of auxins in the presence of precursor L-tryptophan in the medium, which was 184 fold higher than that without L-tryptophan. Ahmad *et al*. (2008) [4] reported auxin levels of 2.13 and 3.6 mgl^{-1} for *Azotobacter* and *Pseudomonas species*, whereas Gravel *et al*. 2007 reported 3.3 and 6.2$mgl1^{-1}$ auxin for *Pseudomonas putida* and *Tricoderma atroviride* respectively.

Phosphorus Solubilization

Phosphorus plays a vital role as the second most important essential macronutrients for biological growth and development after nitrogen, is abundantly available in soils in both organic and inorganic forms (Ahmad and Kibret 2014) [3]. Moreover the substantial amount of phosphorus present in soil ranging from 400 to 1200 mg kg^{-1} of soil either in inorganic (hydroxyapatite, oxyapatite and apatite) or in organic forms (phosphomono esters, phosphodiesters including phospholipids, nucleic acids and inositol phosphate) (Ahemad *et al*. 2008) [4]. It is estimated that rhizosphere soils may constitute a significant proportion (20-40%) of culturable phosphorus solubilizing microorganisms (PSM) (Olander and Vitousek 2004) [68]. In addition organic matter is an important reservoir of immobilized phosphorus that accounts for 20–80% of soil phosphorus (Rodriguez *et al*. 2006) [78]. PSM not only promote plant growth through nitorgen fixation, production of phytohormone siderophores and vitamins, but also provide protection against phytopathogens through the production of antibiotics, HCN, phenazines and antifungal metabolites (He *et al*. 2010; Misra *et al*. 2012; Oves *et al*. 2013; Singh *et al*. 2013) [60, 69, 86]. Increasing amount of pollutants in soil generally interfere with nutrient uptake such as phosphorus and lead to plant growth retardation (Zaidi *et al*. 2009) [100]. This deficiency can be recovered by the phosphate solubilizing ability of PGPR strains. Bacteria belonging to genera *Bacillus*, *Pseudomonas*, *Serratia*, *Enterobacter* are reported to solubilize the insoluble phosphate compounds and aid in plant growth (Kumar *et al*. 2008; Stein 2005). It further substantiates the work (Kumar *et al*. 2011; Dey *et al*. 2004) [55, 25] suggested the effect of phosphate-solubilizing and phytohormone-producing *Azotobacter chroococcum*, *Rhizobium leguminosarum*, *Penicillium rugulosum*, *Pseudomonas fluorescens* in glasshouse or field conditions to enhance yield of wheat, and peanut.

Siderophore production

Iron is a vital nutrient for all living entities with the exception of certain, *Legionella*, *Neisseria*, and *Sacchoromyces cervisiae* (Neilands 1995) [65]. Most organisms require iron as an essential element, it serves as a cofactor for a wide variety of cellular processes, such as electron transport chain, oxygen transport, cellular respiration, chlorophyll biosynthesis, thylakoid biogenesis and chloroplast development (Nishio *et al*. 1988; Kobayashi and Nishizawa 2012) [67, 46]. More than 100 enzymes involve in primary and secondary metabolic reactions contain ferric residues such as iron-sulfur clusters (Miethke and Marahiel 2007) [56]. Although iron is abundantly present in the environment, but the low solubility and slow dissolution rates of iron-containing minerals often limit the bioavailability of iron (Rajkumar *et al*. 2010) [76]. Microorganisms elaborate a variety of low molecular weight organic compounds, with specific affinity to Fe (III) iron, are known as siderophores. Moreover 500 different siderophores have been identified from various organisms ranging from microbes to plants (Boukhalfa and Crumbliss 2002) [17].

The rhizoremediation of soils by PGP microorganisms is believed to reduce chemical fertilizers in agriculture practices (De-Freitas 2000) [22]. Plant growth promotion by siderophore producing rhizobacterial inoculations have been reported in various studies (Rajkumar *et al*. 2010; Meyer 2000; Kumar *et al*. 2013) [76, 59]. Siderophore-producing bacteria *Pseudomonas* strain GRP3 have been shown to enhance chlorophyll content and iron nutrition in *Vigna radiata* plants (Sharma *et al*. 2003) [85]. Fe-Siderophore complex, which is produced by rhizosphere microorganisms, can deliver iron to plant through specific transporter channels under iron starvation (Crowley and Kraemer 2007) [20]. Moreover chelation of trace elements by bacterial siderophores in the rhizosphere have employed as natural biodegradable chelators (Dimkpa *et al*. 2009) [26]. Some siderophores, e.g, desferal, desferrioxamine B, dexrazoxane, O-trensox, desferriexochelins, desferrithiocin, tachpyridine, found useful in sickle cell disease, thalassemia, malaria, haemochromatosis and cancer therapy. Plant growth promotion by siderophore producing rhizobacterial inoculations have been reported in various studies (Rajkumar *et al*. 2010; Meyer 2000; Kumar *et al*. 2013) [76, 59].

Stress hormone Ethylene

The hormone Ethylene, one of the essential metabolite (produced in the end of methionine cycle), found in all higher plants with biological activity at 0.05μlL^{-1} concentration, is an important modulator of plant growth (Glick 2005; 2014). Apart from being a plant growth regulator, ethylene has also been established as potent stress hormone (Saleem *et al*. 2007; Ahemad and Kibret 2014) [82, 3]. Many of the biological functions triggered by ethylene including seed germination, tissue differentiation, formation of root and shoot, root elongation (Montero-Calasanz *et al*. 2013) [61], lateral bud formation, flowering initiation, anthocyanin synthesis, flower senescence, fruit ripening, aroma production, and leaf and fruit abscission. Mutual association with beneficial mycorrhizal fungi and response to biotic and abiotic stresses such as plant response to heavy metals, ozone, pathogens and flooding are several other functions of stress hormone (Tank and Saraf 2009) [92].

1-aminocyclopropane-1-carboxylate deaminase *denovo* synthesis

Plant growth-promoting bacteria colonize to the root surface of a developing plant. In response to tryptophan exudates, bacteria synthesize auxin and facilitate cell proliferation and elongation in host plant. Bacterial auxins together with auxin synthesized by host plant can initiate the formation of 1-aminocyclopropane-1-carboxylate (ACC) synthase to produce ACC (Penrose and Glick 2001) [72]. Plant growth promoting rhizobacteria possess the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase and facilitate plant growth by alleviating ethylene levels. ACC deaminase cleaves ethylene precursor ACC, into ammonia and α-ketobutyrate compounds that are readily further metabolized by the bacteria (Figure 3).

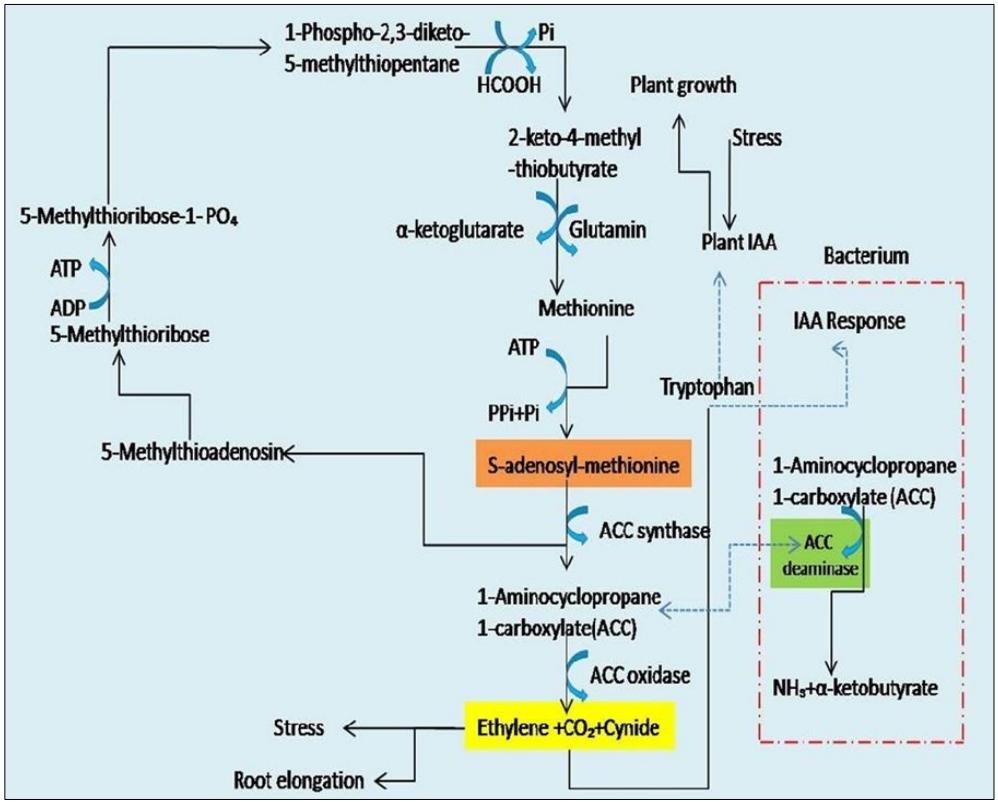

Fig 3: Biosynthetic pathway of ethylene regulation by ACC deaminase action. The figure illustrates the influence of bacteria indole-3-acetic acid (IAA) and1-aminocyclopropane-1-carboxylate (ACC) deaminase on ethylene stress hormone. Bacterial IAA either enhance root growth or increase the synthesis of ethylene (at a low concentration ethylene is important for growth and development but at high concentrations it triggers a stress response in plants). Bacterial ACC deaminase can divert ACC from the ethylene synthesis pathway and metabolize it into inert by-products

Ethylene (stress hormone) is synthesized from S-AdoMet (S-adenosyl methionine) and non-protein amino acid ACC via methionine cycle (Glick 2005; 2014; Ahemad and Kibret 2014) [31, 3].

The conversion of S-AdoMet to ethylene is facilitated by two key enzymes, ACC synthase and ACC oxidase. The rate-limiting factor of ethylene synthesis is ACC synthase because ACC is the immediate precursor to ethylene (Bleecker and Kende 2000) [13]. Besides the activity of ACC deaminase in alleviating ethylene-mediated stresses, ACC deaminase producing rhizobacteria also possess biocontrol potentials by producing HCN (hydrocyanic acid), and some other enzymes like cellulose, chitinase and β-1, 3 glucanase against the fungal pathogens. For instance; the reduced ethylene biosynthesis in tomato plants transformed with bacterial ACC deaminase from *Enterobacter cloacae* decreased disease symptoms of Verticillum wilt (Robison *et al*. 2001) [77]. Various stresses like salt stress, flooding stress, heavy metals and pathogen stress relieved by ACC deaminase producing rhizobacteria were reported frequently (Grichko *et al*. 2000; Grichko and Glick 2001; Mayak, Tirosh and Glick 2004) [33, 32, 57].

Future prospects and Limitations

Further studies on improving the expression of signals that plant and microbes exchange when they recognize each other, selection of the best plant–microbe combinations and expression of catabolic genes during bioremediation of pollutants into field strategies will have to be dissected that can demonstrate the usefulness of this approach. PGPR approach to promote food security also raises the issue such as climatic variations, biotic and abiotic factors that pose challenges in successful application of PGPR as commercial biofertilizer and biocontrol agent. The dynamics of PGPR effects in relation to the host crop, the midterm and long-term effects, the crop-rotation effect, and site variation are still not understood and need to be further investigated.

Additionally various varieties of PGPR have been investigated and some of them have been commercialized, including the species *Azobacter*, *Azosprillum*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Serratia* and *Variovorax*. However, the utilization of PGPR in the agriculture industry represents only a small fraction of agricultural practice worldwide due to the inconsistent properties of the inoculated PGPR, which could influence crop production. Another challenge is the mode of action of PGPR is diverse and not all rhizobacteria possess the same mechanisms. These drawbacks limit the application of PGPR. Therefore, the competition between synthetic chemical fertilizers and PGPR biofertilizer is deemed redundant in the face of the global agricultural productivity needed to feed the booming world's population. The successful utilization of PGPR is dependent on survival in soil, the compatibility with the crop on which PGPR is inoculated, the interaction ability with indigenous microflora in soil, and environmental factors. Measures must be taken to avoid non target effect of the introduced bacteria, to stabilize them in soil systems, and thus to guarantee durability of beneficial effect and good performance of introduced plant growth promoting rhizobacterial inoculants.

Conclusion

Research into the mechanisms of plant growth promotion by rhizosphere bacteria not only provided a relatively reliable method for improved food quality and soil heath but also suggested bioremediation potentials by detoxifying pollutants

like, heavy metal containing agrochemicals and pesticides. The commercial use of PGPR as an integral component of agricultural practice is being used successfully in various developing countries. This is very important to match appropriate PGPR with the right plant and environmental condition to achieve the best results on plant growth. In addition the more effort should be done for the development of good inoculant delivery systems that facilitate the environmental persistence of the PGPR.

Disclosure statement

No potential conflict of interest was reported by the author.

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