

Plant Growth Promoting Bacteria: Biodiversity and Multifunctional Attributes for Sustainable Agriculture



Ajar Nath Yadav^{1*}, Priyanka Verma², Bhanumati Singh³, Vinay Singh Chauahan³, Archana Suman⁴ and Anil Kumar Saxena⁵

¹Department of Biotechnology, Akal College of Agriculture, Eternal University, India

²Department of Microbiology, Akal College of Basic Science, Eternal University, India

³Department of Biotechnology, Bundelkhand University, India

⁴Division of Microbiology, Indian Agricultural Research Institute, India

⁵ICAR-National Bureau of Agriculturally Important Microorganisms, India

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*Corresponding author: Ajar Nath Yadav, Department of Biotechnology, Akal College of Agriculture, Eternal University, India, Tel: +91-9882545085; Email: ajarbiotech@gmail.com

Ajar Nath Yadav and Priyanka Verma contributed equally to the present work.

Abstract

The use of plant growth promoting bacteria may prove useful in developing strategies to facilitate plant growth under normal as well as diverse abiotic stress conditions. The application of microbes with the aim of improving nutrients availability for plants is an important practice and necessary for sustainable agriculture. During the past couple of decades, the use of microbial inoculants for sustainable agriculture has increased tremendously in various parts of the world. Significant increases in growth and yield of agronomically important crops in response to inoculation with plant growth promoting (PGP) microbes have been repeatedly reported. The actual biodiversity of PGP microbes belong to different groups including Actinobacteria, Bacteroidetes, Balneolaeota Firmicutes, Proteobacteria and Spirochaetes. PGP bacteria are naturally occurring soil bacteria that aggressively colonize plant roots and benefit plants by providing growth promotion either directly by solubilization of phosphorus, potassium and zinc; production of indole acetic acids, gibberellic acid, cytokinin; biological nitrogen fixation or in-directly by production of ammonia, hydrogen cyanide, siderophore and biocontrol against different plant pathogens. In this review, we have discussed method of isolation, characterization, identification and biodiversity of bacteria associated with crops and further mechanisms of plant growth promotion under the normal as well as diverse abiotic stress conditions.

Keywords: Abiotic stress; Biodiversity; Crop improvement; Plant growth promotion; Sustainable agriculture

Introduction

To provide food security to the ever increasing population greater agriculture production is a pressing need in 21st century. The increasing demand for a steady and healthy food supply by a burgeoning human population will require efficient management practices along with controlling disease that reduce crop yield. During last few decades, agricultural production has increased due to the use of high yielding varieties and enhanced consumption of chemicals, which are used both as fertilizers to provide nutrition and as protection agents to control the damage caused by phytopathogens. Excessive use of chemicals and change in traditional cultivation practices has resulted in the deterioration of physical, chemical and biological health of the cultivable soil.

Globally need to increase agricultural production from a steadily decreasing and degrading land resource base has placed

significant strain on the delicate agro-ecosystems. Current strategies to maintains and enhanced agricultural productivity via high input practices places considerable emphasis on 'failsafe' techniques for each component of the production sequence with little consideration to the integration of these components in a holistic, systems approach. The use of chemical fertilizers is considered the quickest and surest way of boosting crop production, their cost and other constraints deter farmers from using them in recommended quantities. Various studies report the projections of impact of climate change on different crops production under different simulation models in different continents [1,2]. Under various climate change scenarios the major influencing factor is availability and management of soil water reserves of winter wheat, especially in frequently occurring extreme events such as heat waves and droughts with decrease in annual soil and groundwater recharge [3-6]. However, it is expected that future climate change will affect

wheat yields. This is due to the opposing effects of temperature, salt, pH and drought.

Microbial diversity in soil is considered important for maintaining for the sustainability of agriculture production systems. However, the links between microbial diversity and ecosystem processes is not well understood. Region of contact between root and soil where soil is affected by roots is designated as "rhizosphere". The rhizosphere is the zone of soil influenced by roots through the release of substrates that affect microbial activity. The rhizoplane is the surface, including the strongly adhering soil particles. Root colonizing bacteria that exert beneficial effect on plant development via direct or indirect mechanisms have been defined as plant growth promoting bacteria [7-10]. The concept of plant growth promoting bacteria is now well established both for growth promotion and biocontrol. Plant growth promoting bacteria were first defined by Kloepper & Schroth [11] to describe soil bacteria that colonize the roots of plants following inoculation onto seed and they enhance plant growth. The ineffectiveness of PGP bacteria in the field has often attributed to their inability to colonize plant roots [12-14]. The crops associated bacterial has been extensively investigated in the past few years with a focus on culture dependent techniques and PGP bacteria have been reported e.g. *Agrobacterium*, *Allorhizobium*, *Arthrobacter*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Bradyrhizobium*, *Burkholderia*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Exiguobacterium*, *Flavobacterium*, *Mesorhizobium*, *Micrococcus*, *Providencia*, *Pseudomonas*, *Rhizobium* and *Serratia* [6,15-17]. In addition to understanding the mechanisms of the interaction between plants and microorganisms, colonization mechanisms and strategies represent an important aspect of the interaction. Successful colonization of a PGPB inoculants strain is a requirement to promote plant growth or soil health. This review focuses on bacterial biodiversity, its characterization and mechanisms of PGP under normal as well as abiotic stress conditions.

Isolation and characterization of plant growth promoting bacteria

The microbial communities associated with crops growing in diverse abiotic stress condition have been received much attention, because the food security to the ever increasing population greater agriculture production is a pressing need in 21st century. The microbes associated the crops can be characterized using culture-dependent techniques. The microbes could be isolated using enrichment and serial dilution methods followed by spread or pour plates technique [18]. The rhizospheric, endophytic and phyllospheric microbes can be isolated using standard method of serial dilution, surface sterilization and leaf imprinting techniques [19]. The different

specific and selective growth mediums should be used to isolate the maximum possible culturable morphotypes different genera such as *Arthrobacter* (trypticase soy agar), BBDG (T3 agar), *Methylobacterium* (Ammonium mineral salt), N₂-fixing bacteria (Jensen N₂-free agar), *Pseudomonas* spp. (Kings' B agar), *Rhizobium* (Congo red yeast mannitol) and soil-specific actinobacteria (soil extract agar) [20]. The isolated microbes should be screened for tolerances to different abiotic stresses of salinity, pH, temperature and drought [21].

To know the PGP ability and other potential application of bacteria should be screened qualitatively for direct-PGP attributes which included solubilization of phosphorus [22], potassium [23] and zinc [24]; production of phytohormones indole-3-acetic acid [25], gibberellic acid [26]; biological N₂-fixation [27] and 1-aminocyclopropane-1-carboxylate (ACC) deaminase [28]. The bacteria should be also screened for qualitatively in-direct PGP attributes which included production of ammonia [29], HCN [30], siderophore [31], lytic enzyme [32] and biocontrol against different fungal pathogens [33]. After qualitatively screening the selected bacteria with PGP attributes should be quantitatively screened for N₂-fixing attributes by using the acetylene reduction assay (ARA) [34], P-solubilization [35] K-solubilization [9] and IAA production [36].

For the molecular characterization, the genomic DNA should be isolated from purified pelleted microbial cells of 1.5mL broth should be washed 2-3 times in 1.0mL of TE Buffer (10mM Tris HCl and 1mM EDTA pH 8.0). Microbial lysis should be performed using 0.5mL SET buffer (75mM NaCl, 25mM EDTA and 20mM Tris) with 10μL of lysozyme (10mgmL⁻¹) for 30min at 37 °C and 10% SDS with 20mgmL⁻¹ proteinase K for 1h at 55 °C. DNA should be extracted using phenol/chloroform/isoamyl alcohol and aqueous phase can be transferred to a fresh tube. Finally, the washed DNA pellet should be incubated at 37 °C for 25-30min to completely remove ethanol and then resuspended in 50μL of TE buffer. The amount of DNA extracted should be electrophoresed on 0.8% agarose gel [37]. The universal 16S rRNA gene primers should be used for the amplification of conserved genes. The PCR amplified 16S rRNA gene should be purified with a Quiaquick purification kit (Qiagen). The partial 16S rRNA gene sequences should be compared with those available in the NCBI databases. Identification at the species level was determined using a 16S rRNA gene sequence similarity of ≥97% with that of a prototype strain sequence in the GenBank. Sequence alignment and comparison can perform, using the program CLUSTAL W. The phylogenetic tree can be constructed on the aligned datasets using the neighbor-joining method implemented in the program MEGA 4.0.2 [38]. A schematic representation of the isolation, characterization and identification of plant growth promoting bacteria have presented in Figure 1.

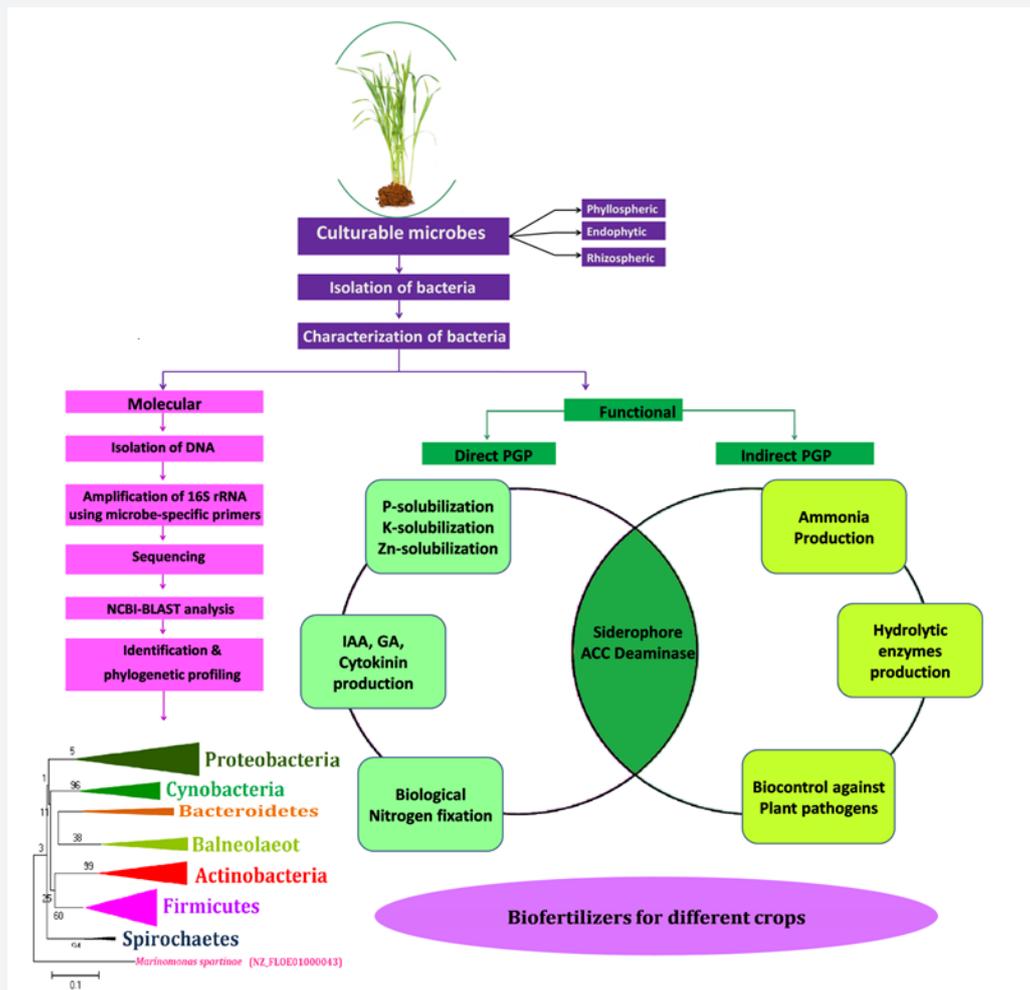


Figure 1: A schematic representation of the isolation, characterization plant growth promoting bacteria.

Plant-microbe interactions

Plant-microbe interactions may be beneficial or harmful, depending on the characteristics of the bacteria involved and the ways in which they interact with plants. Among such microbes, PGP bacteria are distributed on plant roots or in the surrounding soil and have beneficial effects on plants [13]. PGP microbes may promote plant growth, thus providing high crop yields, and they also function as biocontrol agents against plant diseases caused by phytopathogenic microbes. Moreover, recent studies indicate that PGP microbes are able to boost plant tolerance to abiotic stresses such as salinity, temperature, pH and drought [5,9,39]. The PGP bacteria with multifunctional attributes can be used to replace chemical fertilizers and pesticides that are agents of pollution.

PGP bacteria produce a wide range of metabolites that regulate cell content according to ambient biotic and abiotic stresses e.g. some produce hormones such as indole acetic acids (IAAs), ethylene, and gibberellins that enhance plant growth, seed germination, and root growth. Rhizosphere bacteria are also able to fix nitrogen symbiotically and to solubilize mineral phosphates, potassium and zinc. Plant growth promotion by PGP bacteria requires a close relationship between the bacteria and their host plants. This interaction may be recognized as rhizospheric or endophytic [40,41]. During the PGP microbial colonization process, bacteria first occupy the rhizosphere. Endophytes are then able to enter plant tissues through the root zone, after which they penetrate plant cells, often conferring beneficial effects on hosts [41]. Biological control is achieved through mechanisms such as parasitism, competition and antibiosis which adversely affect the fitness, survival and reproduction of nematodes (Figure 2).

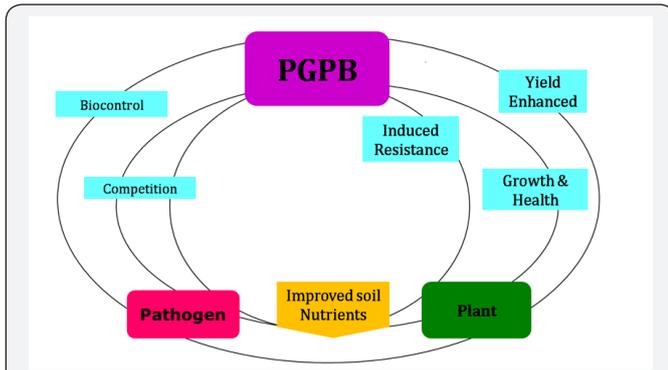


Figure 2: Plant microbes-interactions and their action of plant growth promotion.

Biodiversity of plant growth promoting bacteria

Biodiversity is defined as the variety of living organisms at species, inter-species and intra-species level in ecology. Microbes are quite beneficial and exploited in gain of quite lot

revenue for sustainable agriculture and human health. Microbial diversity in rhizospheric soil ecosystem exceeds more than eukaryotic organisms. One gram of soil may harbor up to 10 billion microbiomes of possible thousands of different species, and thus the rhizosphere of any plant is hot spot of biodiversity of microbes (archaea, bacteria and fungi). On review of different research on biodiversity of microbes associated with crops, it was found that microbes belonged to different phylum mainly: *Actinobacteria*, *Bacteroidetes*, *Balneolaeta*, *Basidiomycota*, *Cyanobacteria*, *Firmicutes*, *Proteobacteria* and *Spirochaetes*. Among all reported phylum the members of phylum Firmicutes were most dominant followed by Proteobacteria (Figure 3). The Proteobacteria were further grouped as α , β , and γ -proteobacteria. These microbes been reported from cereal crops (Wheat, rice, maize, sugarcane, chick pea etc.) [17,27,42-45]. The microbes have beneficial ecological significance as they have been reported as common as well as niche or host-specific. The niche of host-specific microbes may play important role in vegetation of specific plants in different abiotic stress regions.

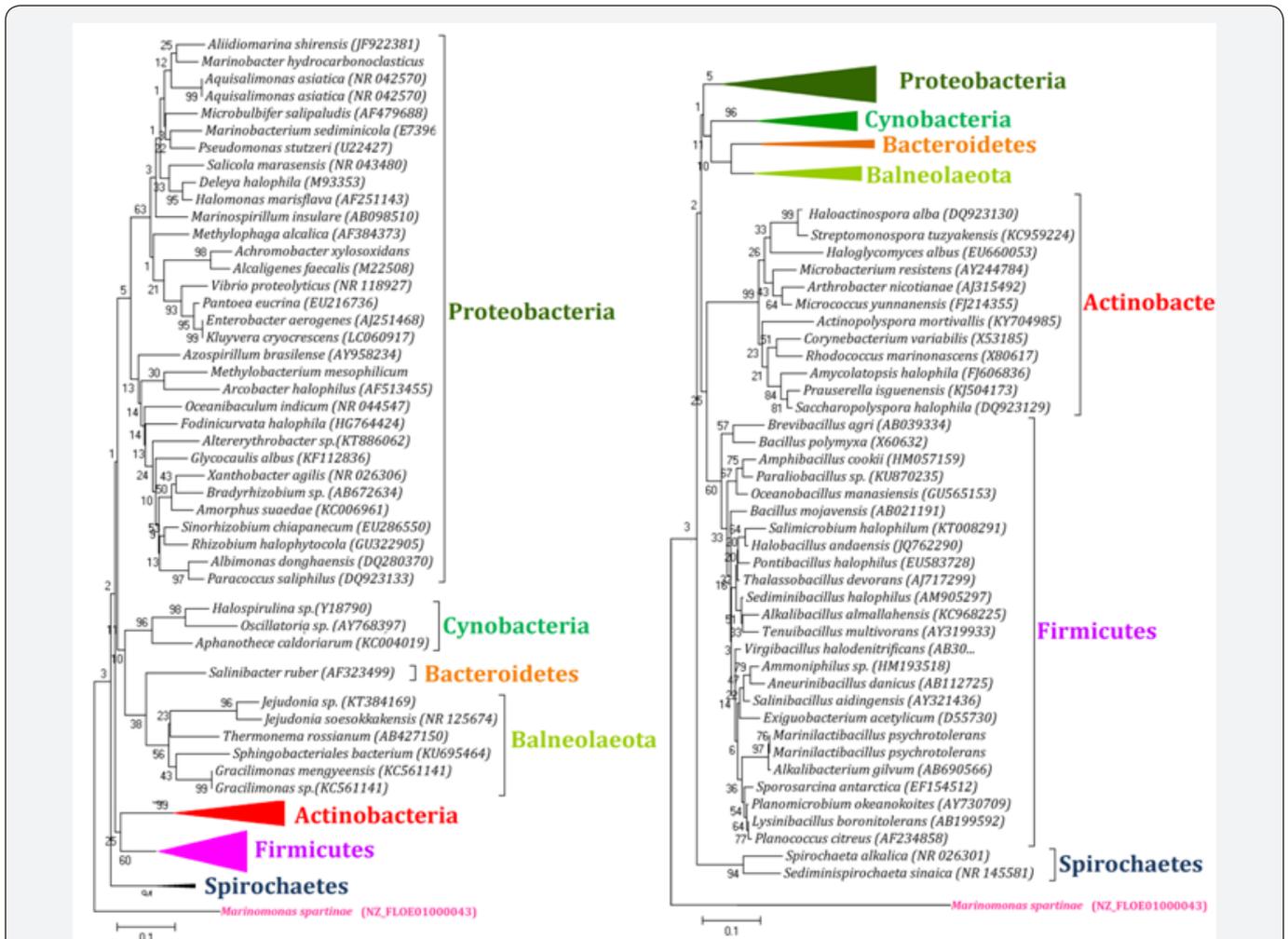


Figure 3: Phylogenetic tree showed the relationship among different groups of bacteria.

Actinobacteria

Actinobacteria are of agriculturally important as they can enhance plant growth; improve plant nutrition through direct plant growth promoting. Several studies have indicated that Actinobacteria colonization can also result in increased plant vigor, and it confers tolerance to biotic and abiotic stresses, enhanced drought tolerance, and improved nutrients utilization [36,46]. On review diversity of actinobacteria associated with different crops all 6-classes have been reported, whose phylogenetic investigations have been carried out mainly by using 16S rRNA gene sequences. On review of different crops, it was found that microbes were most predominant and studied belong to all six classes in which many bacteria like *Arthrobacter*, *Brevibacterium*, *Cellulomonas*, *Corynebacterium*, *Kocuria*, *Microbacterium*, *Micrococcus*, *Mycobacterium*, *Rhodococcus* and *Streptomyces* have been reported from all crops reviewed.

In rhizospheric soil, Actinobacteria represents a high proportion of the microbial biomass. Their populations are found at 10^9 - 10^6 bacteria per gram of soil and they represent more than 30% of total population of soil microbiomes. Among different genera of actinobacteria two genera namely *Streptomyces* and *Nocardia* have been well represented in rhizospheric soil. It has been reported that *Streptomyces* may be represent about >95% of the whole soil Actinobacterial microbiomes. The members of Actinobacteria play a major role in agricultural soil quality and soil fertility. Actinobacteria represents a large fraction of microbiomes in the root systems and is well established that they are dominant fraction of the microbial community in soils of wild and agricultural plant species [47-51]. Together with other phyla, the members of actinobacteria account for a large proportion in the rhizosphere of numerous plants including wheat (*Triticum aestivum*) [9,17,44,52,53]; rice (*Oryza sativa*) [48,54,55]; maize (*Zea mays*) [50,56,57]; Sugarcane (*Saccharum officinarum*) [58-60]; soybean (*Glycine max*) [51,61-63]; pea (*Pisum sativum*) [51,64,65]; sunflower (*Helianthus annuus*) [49,66,67] and chickpea (*Cicer arietinum*) [68,69].

Firmicutes

The member *Bacillus* and *Bacillus* derived genera (BBDG) belonged to phylum Firmicutes are associated with different plant, show different plant growth promoting attributes. Among bacilli, *Bacillus* and *Paenibacillus* are the most dominant genera followed by *Alicyclobacillus*, *Aneurinibacillus*, *Virgibacillus*, *Salibacillus*, and *Gracilibacillus* reported from different crops plants [32,33]. Garbeva et al. [70] showed that the majority (95%) of Gram-positive bacteria in soils under different types of management regimes (permanent grassland, grassland turned into arable land, and arable land), were putative *Bacillus* species; *B. mycooides*, *B. pumilus*, *B. megaterium*, *B. thuringiensis*, and *B. firmus*, as well as related taxa such as *Paenibacillus*, were frequently identified by sequencing the DNA bands obtained on DGGE gels. Bacteria of the genus *Bacillus* Cohn are widely

dispersed in nature, easy to multiply, have a long shelf life when sporulated and are nonpathogenic. *Bacillus subtilis*, *B. mycooides*, *B. pumilus*, *B. megaterium*, *B. thuringiensis* and *B. firmus* are wide range of *Bacillus* present in rhizosphere soil [9,17,52,53].

Verma et al. [52], investigated forty one endophytic bacteria were isolated from surface-sterilized roots and culms of wheat var. HS507, growing in NW Indian Himalayas. These bacteria were screened *in vitro* for multifarious plant growth promoting attributes such as solubilization of phosphorus, potassium, zinc; production of indole acetic acids, hydrogen cyanide, gibberellic acid, siderophore and activities of nitrogen fixation, ACC deaminase and biocontrol against *Rhizoctonia solani* and *Macrophomina phaseolina* at low temperature (4 °C). One isolate IARI-HHS2-30, showed appreciable level of potassium solubilization was further characterized *in vivo* at control condition of low temperature. Based on 16S rDNA sequence analysis, this isolate was identified as *Bacillus amyloliquefaciens* assigned accession number KF054757. Analysis of the phylogenetic characterization showed close homology with typical psychrotolerant bacteria *Bacillus amyloliquefaciens*, *B. methylotrophicus*, *B. polyfermenticus*, *B. siamensis*, *B. subtilis*, and *B. vallismortis*. Endophytic nature and plant growth promoting ability of IARI-HHS2-30 was tested by qualitatively and followed by inoculation onto wheat seedlings in low temperature conditions. At 30 days after inoculation, *Bacillus amyloliquefaciens* IARI-HHS2-30 to wheat plants resulted in significant increase in root/shoot length, fresh weight, and chlorophyll a content. Plant growth promoting features coupled with psychrophilic ability suggest that this endophytic bacterium may be exploited as bio-inoculants for various crops in low temperature and high altitude condition.

Yadav et al. [33], reported and characterized psychrotrophic Bacilli from different sites in north western Indian Himalayas. A total of 247 morphotypes were obtained from different soil and water samples and were grouped into 43 clusters based on 16S rDNA-RFLP analysis. Sequencing of representative isolates from each cluster led to their identification and 43 Bacilli belonged to different species of eleven genera *viz.* *Desemzia*, *Exiguobacterium*, *Jeotgalicoccus*, *Lysinibacillus*, *Paenibacillus*, *Planococcus*, *Pontibacillus*, *Sinobaca*, *Sporosarcina*, *Staphylococcus* and *Virgibacillus*. With an aim to develop microbial inoculants that can perform efficiently at low temperatures, all representative isolates were screened for different plant growth promoting traits at low temperatures (5-15 °C). Among the strains, variations were observed for production of ammonia (22%), indole-3-acetic acid (20%), siderophores (8%), gibberellic acid (4%) and hydrogen cyanide (3%); solubilization of phosphate (12%), zinc (16%) and potassium (8%); 1-aminocyclopropane-1-carboxylate deaminase activity (5%) and biocontrol activity (19%) against *Rhizoctonia solani* and *Macrophomina phaseolina*. Among all the strains *Bacillus licheniformis*, *Bacillus muralis*, *Desemzia incerta*, *Paenibacillus tylopili* and *Sporosarcina*

globispora were found to be potent candidates to be developed as inoculants as they exhibited multiple PGP traits at low temperature.

Verma et al. [9] investigated culturable Bacilli in six wheat cultivating agro-ecological zones of India viz: northern hills, north western plains, north eastern plains, central, peninsular and southern hills. These agro-ecological regions are based on the climatic conditions such as pH, salinity, drought and temperature. A total of 395 Bacilli were isolated by heat enrichment and different growth media. Phylogenetic analysis based on 16S rRNA gene sequencing led to the identification of 55 distinct Bacilli that could be grouped in five families, Bacillaceae (68%), Paenibacillaceae (15%), Planococcaceae (8%), Staphylococcaceae (7%) and Bacillales incertae sedis (2%), which included eight genera namely *Bacillus*, *Exiguobacterium*, *Lysinibacillus*, *Paenibacillus*, *Planococcus*, *Planomicrobium*, *Sporosarcina* and *Staphylococcus*. All 395 isolated Bacilli were screened for their plant growth promoting attributes, which included direct-plant growth promoting (solubilization of phosphorus, potassium and zinc; production of phytohormones; 1-aminocyclopropane-1-carboxylate deaminase activity and nitrogen fixation), and indirect-plant growth promotion (antagonistic, production of lytic enzymes, siderophore, hydrogen cyanide and ammonia). To our knowledge, this is the first report for the presence of *Bacillus endophyticus*, *Paenibacillus xylanexedens*, *Planococcus citreus*, *Planomicrobium okeanoikoites*, *Sporosarcina* sp. and *Staphylococcus succinus* in wheat rhizosphere and exhibit multifunctional PGP attributes. These niche-specific and multifarious PGP Bacilli may serve as inoculants for crops growing in respective climatic conditions.

Proteobacteria

The phylum proteobacteria are a major group of Gram-negative bacteria which included $\alpha/\beta/\gamma$ - proteobacteria. The γ -proteobacteria is the largest class in terms of species *Pseudomonas* and *Azotobacter*. *Azotobacter* is a gram-negative, aerobic, heterotrophic, rod shaped nitrogen fixing bacteria present in alkaline and neutral soils. They are free living organism present in soil, water and also in association with some plants [71-74]. Various species of *Azotobacter* such as *A. agilis*, *A. chroococcum*, *A. beijerinckii*, *A. vinelandii*, *A. ingrinis* has been reported from different crops. Among proteobacteria most dominant and plant growth promoting genera belong to *Pseudomonas*. *Pseudomonas* is a genus of Gram-negative, aerobic γ -proteobacteria, belonging to the family Pseudomonadaceae and containing 191 validly described species. The certain members of the *Pseudomonas* genus have been applied to cereal seeds or applied directly to soils as a way of preventing the growth or establishment of crop pathogens. The biocontrol properties of *P. fluorescens* and *P. protegens* are currently best-

understood, although it is not clear exactly how the plant growth-promoting properties of *P. fluorescens* are achieved. Other notable *Pseudomonas* species with biocontrol properties include *Pseudomonas*, which produces a phenazine-type antibiotic active agent against certain fungal plant pathogens [75].

Verma et al. [20], reported 135 wheat associated plant growth promoting bacteria from acidic soil, among all isolates *Pseudomonas chlororaphis* IARI-THD-13, *Pseudomonas fluorescens* IARI-THD-21, *Pseudomonas rhodesiae* IARI-THD-11 and *Pseudomonas rhodesiae* IARI-THD-28 exhibited direct and indirect plant growth promoting attributes. Verma et al. [44], investigated thermotolerant wheat associated plant growth promoting bacteria which has been identified using 16S rRNA gene sequencing. *Bacillus* and *Pseudomonas* were dominant in rhizosphere while *Methylobacterium* were in phyllosphere. Different species of *Pseudomonas fuscovaginae* IARI-IIWP-29, *Pseudomonas lini* IARI-IIWP-33, *Pseudomonas montelii* IARI-IIWP-27, *Pseudomonas stutzeri* IARI-IHD-4 and *Pseudomonas thivervalensis* IARI-IHD-3 have been sort out from wheat as endophytic, rhizospheric as well as epiphytic. Verma et al. [19], reported psychrotolerant wheat associated bacteria from northern hills zone of India. A total 247 bacteria were isolated from five different sites. 16S rRNA gene based phylogenetic analysis, revealed that 65, 26, 8 and 1% bacteria belonged to four phyla namely Proteobacteria, Firmicutes, Actinobacteria and Bacteroidetes respectively. Overall 28% of the total morphotypes belonged to *Pseudomonas* followed by *Bacillus* (20%), *Stenotrophomonas* (9%), *Methylobacterium* (8%), *Arthrobacter* (7%), *Pantoea* (4%), *Achromobacter*, *Acinetobacter*, *Exiguobacterium* and *Staphylococcus* (3%), *Enterobacter*, *Providencia*, *Klebsiella* and *Leclercia* (2%), *Brevundimonas*, *Flavobacterium*, *Kocuria*, *Kluyvera* and *Planococcus* (1%).

Mechanisms of plant growth promotion

Plants play an important role in selecting and enriching the types of bacteria by the constituents of their root exudates. Thus, depending on the nature and concentrations of organic constituents of exudates, and the corresponding ability of the microbes to utilize these as sources of energy, the microbial community have been developed. Microbes associated with crops are of agriculturally important as they can enhance plant growth; improve plant nutrition through biological N_2 -fixation and other mechanisms. The growth stimulation by microbes can be a consequence of biological N_2 -fixation, production of phytohormones, such as IAA and cytokines; biocontrol of phytopathogens through the production of antifungal or antibacterial agents, siderophore production, nutrient competition and induction of acquired host resistance or enhancing the bioavailability of minerals (Table 1; Figure 4).

Table 1: Plant growth prompting bacterial strains isolated from different host plants.

Phylum	Bacterial Strains	Host	References
Actinobacteria	<i>Actinomyces</i> sp., <i>Agromyces</i> sp., <i>Arthrobacter agilis</i> , <i>Arthrobacter humicola</i> , <i>Arthrobacter methylotrophus</i> , <i>Arthrobacter nicotinovorans</i> , <i>Arthrobacter</i> sp., <i>Brevibacterium epidermidis</i> , <i>Cellulosimicrobium</i> sp., <i>Corynebacterium callunae</i> , <i>Kocuria kristinae</i> , <i>Micrococcus luteus</i> , <i>Providencia alcalifaciens</i> , <i>Streptomyces acidiscabies</i> , <i>Streptomyces albovinaceus</i> , <i>Streptomyces carnosus</i> , <i>Streptomyces cyaneofuscatus</i> , <i>Streptomyces elanosporofaciens</i> , <i>Streptomyces enissocaesilis</i> , <i>Streptomyces flavotricini</i> , <i>Streptomyces griseus</i> , <i>Streptomyces kanamyceticu</i> , <i>Streptomyces Kunmingensis</i> , <i>Streptomyces mutabilis</i> , <i>Streptomyces scabrisporus</i> , <i>Streptomyces violaceusniger</i> , <i>Streptomyces viridificanswas</i> , <i>Zhihengliuella alba</i>	Cowpea, Millet, Mustard, Wheat	[9,17-20,44,52,53,82,116-123-128]
Bacteroidetes	<i>Flavobacterium psychrophilum</i> , <i>Flavobacterium</i> sp., <i>Sphingobacterium</i> sp., <i>Chryseobacterium humi</i>	Barley, Millet, Wheat	[6,44,129-132]
Firmicutes	<i>Bacillus aerophilus</i> , <i>Bacillus alcalophilus</i> , <i>B. altitudinis</i> , <i>B. amyloliquefaciens</i> , <i>B. aquimaris</i> , <i>B. cereus</i> , <i>B. circulans</i> , <i>B. endophyticus</i> , <i>B. flexus</i> , <i>B. fusiformis</i> , <i>B. licheniformis</i> , <i>B. megaterium</i> , <i>B. methylotrophicus</i> , <i>B. mojavensis</i> , <i>B. pumilus</i> , <i>B. solisalsi</i> , <i>B. sphaericus</i> , <i>B. subtilis</i> , <i>B. tequilensis</i> , <i>B. thuringiensis</i> , <i>Brevibacterium halotolerans</i> , <i>Exiguobacterium acetylicum</i> , <i>Lysinibacillus fusiformis</i> , <i>Lysinibacillus xylanilyticus</i> , <i>Paenibacillus alvei</i> , <i>Paenibacillus dendritiformis</i> , <i>Paenibacillus lautus</i> , <i>Paenibacillus polymyxa</i> , <i>Paenibacillus xylanexedens</i> , <i>Planococcus citreus</i> , <i>Planococcus rifietoensis</i> , <i>Planococcus salinarum</i> , <i>Planococcus salinarum</i> , <i>Planomicrobium okeanokoites</i> , <i>Staphylococcus equorum</i>	Amaranth, Apple, Barley, Buckwheat, Maize, Mustard, Oat, Pepper, Rice, Sorghum, Sunflower, Tomato, Wheat	[5,9,19,20,42,44,52,53,133-144]
Proteobacteria	<i>Achromobacter piechaudii</i> , <i>Achromobacter xylosoxidans</i> , <i>Acinetobacter</i> sp., <i>Advenella</i> sp., <i>Agrobacterium larrymoorei</i> , <i>Alcaligenes</i> sp., <i>Azotobacter tropicalis</i> , <i>Bradyrhizobium</i> sp., <i>Enterobacter</i> sp., <i>Halomonas korlensis</i> , <i>Hartmannibacter diazotrophicus</i> , <i>Methylobacterium phyllosphaerae</i> , <i>M. radiotolerans</i> , <i>Nitrincola lacisaponensis</i> , <i>Ochrobacterium haematophilum</i> , <i>Pantoea agglomerans</i> sp., <i>Providencia rustigianii</i> , <i>Pseudomonas aeruginosa</i> , <i>Pseudomonas cedrina</i> , <i>Pseudomonas fluorescens</i> , <i>Pseudomonas gessardii</i> , <i>Pseudomonas mendocina</i> , <i>Pseudomonas putida</i> , <i>Pseudomonas rhodesiae</i> , <i>Pseudomonas thivervalensis</i> , <i>Serratia marcescens</i> , <i>Tetrathiobacter</i> sp.	Amaranth, Barley, Buckwheat, Cotton, Cowpea, Gram, Maize, Millet, Mustard, Oat, Rice, Sunflower, Tomato, Wheat	[6,9,14,17,19,43,44,52,53,130,140-147]

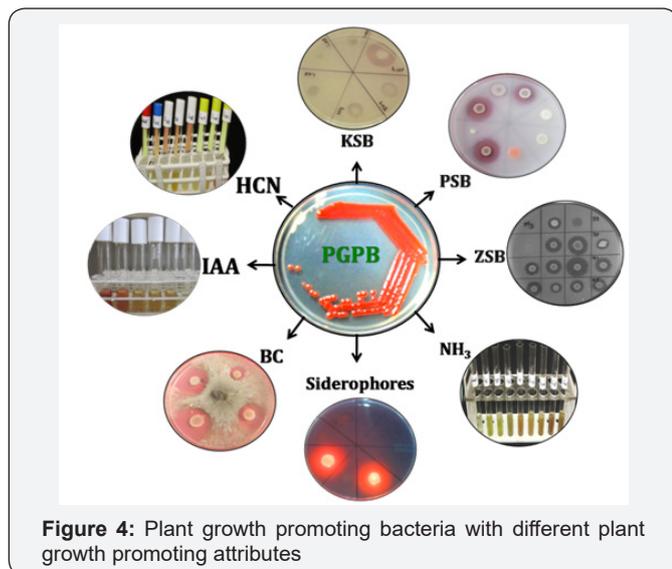


Figure 4: Plant growth promoting bacteria with different plant growth promoting attributes

Indole-3-acetic acid production

Plant hormones are chemical messengers that affect a plant's ability to respond to its environment. Hormones are organic compounds that are effective at very low concentration; they are usually synthesized in one part of the plant and are transported to another location. They interact with specific target tissues to cause physiological responses, such as growth or fruit ripening. Each response is often the result of two or more hormones acting together. Because hormones stimulate or inhibit plant growth, many botanists also refer to them as plant growth regulators. Researchers recognize five major groups of hormones: auxins, gibberellins, ethylene, cytokinins, and abscisic acid [14,76].

IAA (indole-3-acetic acid) is the member of the group of phytohormones and is generally considered the most important native auxin. It functions as an important signal molecule in the regulation of plant development including organogenesis, tropic responses, cellular responses such as cell expansion, division, and differentiation, and gene regulation. Diverse bacterial species possess the ability to produce the auxin phytohormone IAA [77-79]. Different biosynthesis pathways have been identified and redundancy for IAA biosynthesis is widespread among plant-associated bacteria. Interactions between IAA-producing bacteria and plants lead to diverse outcomes on the plant side, varying from pathogenesis to phytostimulation. Verma et al. [19], biodiversity of wheat-associated bacteria from the northern hills zone of India was deciphered. A total of 247 bacteria were isolated from five different sites. Among all isolated bacteria 14% showed IAA production in which strain IARI-HHS1-3 showed highest IAA production ($70.8 \pm 1.5 \mu\text{g mg}^{-1} \text{ protein day}^{-1}$) followed by IARI-HHS1-8 ($69.1 \pm 0.5 \mu\text{g mg}^{-1} \text{ protein day}^{-1}$)

Tabatabaei et al. [76], have reported *Pseudomonas* isolated from wheat. An *in vitro* experiment was conducted to observe the effect of the inoculation of four indole-3-acetic acid (IAA)-

producing *Pseudomonas* isolates and exogenous IAA on seed germination traits and α -amylase activity of durum wheat. The results showed inoculation with all bacterial isolates led to a decrease in the germination percent, although the extent of the depression varied with the isolate. A significant relationship between concentrations of bacterial IAA and the germination inhibition percent in durum wheat seeds by different bacteria strains was observed. Several plant growth promoting rhizobacteria *Azotobacter* sp., *Rhizobium* sp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *Pseudomonas fluorescens*, *Bacillus subtilis* and *Paenibacillus polymyxa* can produce cytokinins or gibberellins or both can produce either cytokinins or gibberellins or both for plant growth promotion. Some strains of phytopathogens can also synthesize cytokinins. However, it appears that plant growth promoting bacteria produce lower cytokinin levels compared to phytopathogens so that the effect of the plant growth promoting rhizobacteria on plant growth is stimulatory while the effect of the cytokinins from pathogens is inhibitory.

Phosphate and potassium solubilization

Phosphorus (P) is major essential macronutrients for biological growth and development. Bacteria offer a biological rescue system capable of solubilizing the insoluble inorganic P of soil and make it available to the plants. The ability of some bacteria to convert insoluble phosphorus (P) to an accessible form, like orthophosphate, is an important trait in PGP bacterium for increasing plant yields. The rhizospheric phosphate utilizing bacteria could be a promising source for plant growth promoting agent in agriculture. The use of phosphate solubilizing bacteria as inoculants increases the P uptake by plants. Phosphorus (P) is major essential macronutrients for biological growth and development. P in soils is immobilized or becomes less soluble either by absorption, chemical precipitation, or both. Under such conditions, microorganisms offer a biological rescue system capable of solubilizing the insoluble inorganic P of soil and make it available to the plants. Phosphate solubilizing bacteria include largely bacteria and fungi, which can grow in media containing tricalcium, iron and aluminium phosphate, hydroxyapatite, bonemeal, rock phosphate and similar insoluble phosphate compounds as the sole phosphate source. Such microbes not only assimilate P but a large portion of soluble phosphate is released in quantities in excess of their own requirement.

Phosphate solubilization is a common trait among microbes associated with different crops. For instance, the majority of microbial populations from wheat, rice, maize, and legumes were able to solubilize mineral phosphates in plate assays and A vast number of PGP microbes with phosphate solubilizing property have been reported which include members belonging to *Burkholderia*, *Enterobacter*, *Halolamina*, *Pantoea*, *Pseudomonas*, *Citrobacter* and *Azotobacter* [14,52,80-82]. Possible mechanisms for solubilization from organic bound phosphate involve either enzymes namely C-P lyase, non-specific phosphatases and

phytases. However, most of the bacterial genera solubilize phosphate through the production of organic acids such as gluconate, ketogluconate, acetate, lactate, oxalate, tartarate, succinate, citrate and glycolate.

Verma et al. [9], have reported 395 Bacilli from wheat and these bacteria have been screened for direct and indirect PGP traits. Of 55 representatives, 39, 18, and 40 strains exhibited solubilization of phosphorus, potassium, and zinc respectively. Among P, K, and Zn solubilizers, *Paenibacillus polymyxa* BNW6 solubilized highest amount of phosphorus $95.6 \pm 1.0 \text{ mg L}^{-1}$ followed by *Sporosarcina* sp. BNW4 $75.6 \pm 1.0 \text{ mg L}^{-1}$. *Planococcus salinarum* BSH13 ($46.9 \pm 1.2 \text{ mg L}^{-1}$) and *Bacillus pumilus* BCZ15 ($7.5 \pm 0.5 \text{ mg L}^{-1}$) solubilized highest amount of potassium and zinc respectively.

Potassium (K) is the third major essential macronutrient for plant growth. The concentrations of soluble potassium in the soil are usually very low and more than 90% of potassium in the soil exists in the form of insoluble rocks and silicate minerals. Moreover, due to imbalanced fertilizer application, potassium deficiency is becoming one of the major constraints in crop production. Without adequate potassium, the plants will have poorly developed roots, grow slowly, produce small seeds and have lower yields. This emphasized the search to find an alternative indigenous source of potassium for plant uptake and to maintain potassium status in soils for sustaining crop production [52]. Plant growth promoting bacteria are able to solubilize potassium rock through production and secretion of organic acids. Potassium solubilizing plant growth promoting rhizobacteria such as *Acidithiobacillus ferrooxidans*, *Bacillus edaphicus*, *Bacillus mucilaginosus*, *Burkholderia*, *Paenibacillus* sp. and *Pseudomonas* has been reported to release potassium in accessible form from potassium bearing minerals in soils. Thus, application of potassium solubilizing plant growth promoting bacteria as biofertilizer for agriculture improvement can reduce the use of agrochemicals and support ecofriendly crop production. K-solubilizing bacteria (KSB) were found to resolve potassium, silicon and aluminium from insoluble minerals. Among different groups of microbes, BBDG were best characterized for K-solubilization [52,83]. The K-solubilizing bacteria may have use in the amelioration of K-deficient soil in agriculture. There are only few reports on K-solubilization by endophytic bacteria isolated from wheat [9,20,53].

Biological nitrogen fixation

Nitrogen is the major limiting factor for plant growth, the application of N_2 -fixing microbes as biofertilizers has emerged as one of the most efficient and environmentally sustainable methods for increasing the growth and yield of crop plants. Biological nitrogen fixation (BNF) is one of the possible biological alternatives to N-fertilizers and could lead to more productive and sustainable agriculture without harming the environment. Many associative bacteria are now known to fix atmospheric nitrogen and supply it to the associated host

plants. A variety of nitrogen fixing microbes like *Arthrobacter*, *Azoarcus*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Enterobacter*, *Gluconoacetobacter*, *Herbaspirillum*, *Klebsiella*, *Pseudomonas*, and *Serratia* have been isolated from the rhizosphere of various crops, which contribute fixed nitrogen to the associated plants [84-88].

Choudhury et al. [89], reported that the Azolla and cyanobacteria can supplement the nitrogen requirements of plants, replacing 30-50% of the required urea-N in rice production. BNF by *Azotobacter*, *Clostridium*, *Azospirillum*, *Herbaspirillum* and *Burkholderia* can substitute for urea-N, while *Rhizobium* can promote the growth physiology or improve the root morphology of the rice plant. Green manure crops can also fix substantial amounts of atmospheric N. Among the green manure crops, *Sesbania rostrata* has the highest atmospheric N_2 -fixing potential, and it has the potential to completely substitute for urea-N in rice cultivation. Gtari et al. [90], reported that non-Frankia actinobacteria has dramatically increased and has opened investigation on the origin and emergence of diazotrophy among actinobacteria. During the last decade, *Mycobacterium flavum*, *Corynebacterium autotrophicum* and a fluorescent *Arthrobacter* sp. have been reported to have nitrogenase activity. Verma et al. [44], isolated and characterized drought tolerant nitrogen fixing rhizospheric actinobacteria *Arthrobacter humicola* IARI-IIWP-42 associated with wheat growing in central zone of India. Verma et al. [19], reported the psychrotrophic microbes from wheat rhizosphere growing in northern hills zone of India. *Arthrobacter methylotrophus* IARI-HHS1-1 and *Arthrobacter methylotrophus* IARI-HHS1-25 fixed atmospheric nitrogen 18.25 ± 1.2 and $9.65 \pm 1.5 \text{ nmol ethylene h}^{-1} \text{ mg}^{-1} \text{ protein}$ respectively. Among isolated actinobacteria, three strains were identified as *Arthrobacter methylotrophus*, *Arthrobacter nicotinovorans* and *Kocuria kristinae* exhibited more than six different plant growth promoting activities at low temperature.

ACC-deaminase activity

Ethylene (C_2H_4) an important plant-signaling molecule involves in many plant functions including seed germination, root hair development, root nodulation, flower senescence, leaf abscission and fruit ripening. Ethylene is produced by a two-step process that consists of enzymatic conversion of S-adenosyle methionine (SAM) to ACC followed by the conversion of ACC to ethylene, which is catalyzed by ACC-oxidase. Ethylene production in plants is increased upon exposure to biotic and abiotic stresses, including extreme salinity, temperature, drought, and infection by viral, bacterial and fungal pathogens. It has been investigated that certain microbes contain an enzyme ACC-deaminase which hydrolyses ACC, the precursor of ethylene into ammonia and α -ketobutyrate, thereby reducing the levels of ethylene which can inhibit plant growth. Currently, bacterial strains exhibiting ACC deaminase activity have been identified in a wide range of genera such as *Acinetobacter*,

Achromobacter, *Agrobacterium*, *Alcaligenes*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Pseudomonas*, *Ralstonia*, *Serratia* and *Rhizobium* [19,20,33,44,52,53,91]. Ethylene is a key regulator of the colonization of plant tissue by bacteria which in turn suggests that the ethylene inhibiting effects of ACC-deaminase may be a bacterial colonization strategy. Regardless of why plant-associated bacteria produce ACC-deaminase, their application can clearly be a very useful strategy to mitigate the effects of various stressors on cultivated plants. Generally, ethylene is an essential metabolite for the normal growth and development of plants [92,93]. Under stress conditions like those generated by salinity, drought, water logging, heavy metals and pathogenicity, the endogenous level of ethylene is significantly increased which negatively affects the overall plant growth. Plant growth promoting bacteria which possess the enzyme, 1-aminocyclopropane-1-carboxylate (ACC) deaminase, facilitate plant growth and development by decreasing ethylene levels, inducing salt tolerance and reducing drought stress in plants [20,44,93,94].

Biocontrol

Phytopathogenic microbes are a major and chronic threat to sustainable agriculture and ecosystem stability worldwide subverts the soil ecology, disrupt environment, degrade soil fertility and consequently show harmful effects on human health, along with contaminating ground water. Plant growth promoting bacteria is a promising sustainable and environmentally friendly approach to obtain sustainable fertility of the soil and plant growth indirectly. This approach takes inspire a wide range of exploitation of plant growth promoting bacteria led to reducing the need for agrochemicals (fertilizers and pesticides) for improve soil fertility by a variety of mechanisms that via production of antibiotics, siderophores, HCN, hydrolytic enzymes. Phytopathogenic microorganism can control by releasing siderophores, β -1, 3-glucanase, chitinases, antibiotics, fluorescent pigment or by cyanide production. World agriculture faces a great loss every year incurred from infection by pathogenic organisms. Application of microorganism for the control of diseases seems to be one of the most promising ways. Biocontrol systems are ecofriendly, cost-efficient and involved in improving the soil consistency and maintenance of natural soil flora. To act efficiently, the biocontrol agent should remain active under large range of conditions *viz.*, varying pH, temperature and concentrations of different ions. Biocontrol agents limit growth of pathogen as well as few nematodes and insects. Recent studies have indicated that biological control of bacterial wilt disease could be achieved using antagonistic bacteria. Different bacterial species, namely, *Alcaligenes* sp., *Bacillus pumilus*, *B. subtilis*, *B. megaterium*, *Clavibacter michiganensis*, *Curtobacterium* sp., *Flavobacterium* sp., *Kluyvera* sp., *Microbacterium* sp., *Pseudomonas alcaligenes*, *P. putida*, *P. fluorescens* have been reported as endophytes and were inhibitory to plant pathogens [19,95-100].

Iron is an essential growth element for all living organisms. The scarcity of bioavailable iron in soil habitats and on plant surfaces foments a furious competition. Under iron-limiting conditions PGPB produce low-molecular-weight compounds called siderophores to competitively acquire ferric ion. Siderophores (Greek: «iron carrier») are small, high-affinity iron chelating compounds secreted by microorganisms such as bacteria, fungi and grasses [101-104]. Microbes release Siderophores to scavenge iron from these mineral phases by formation of soluble Fe^{3+} complexes that can be taken up by active transport mechanisms. Many siderophores are non-ribosomal peptides, although several are biosynthesised independently. Siderophores are low molecular weight bio-molecules secreted by micro-organisms in response to iron starvation for acquisition of iron from insoluble forms by mineralization and sequestration. Although some siderophores are known to chelate other ions, their specificity and avidity for iron is the most consistent feature. Many plants can use various bacterial siderophores as iron sources, although the total concentrations are probably too low to contribute substantially to plant iron uptake. Siderophores have been implicated for both direct and indirect enhancement of plant growth by plant growth promoting bacteria. The direct benefits of bacterial siderophores on the growth of plants have been demonstrated by using radio labeled ferric siderophores as a sole source of iron showed that plants are able to take up the labeled iron by a large number of plant growth promoting bacteria including *Aeromonas*, *Azadirachta*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Pseudomonas*, *Rhizobium*, *Serratia* and *Streptomyces* sp. [99,105-107].

Certain bacteria synthesize a wide spectrum of multifunctional polysaccharides including intracellular polysaccharides, structural polysaccharides, and extracellular polysaccharides. Production of exo polysaccharides is generally important in biofilm formation; root colonization can affect the interaction of microbes with roots appendages. Effective colonization of plant roots by EPS-producing microbes helps to hold the free phosphorous from the insoluble one in soils and circulating essential nutrient to the plant for proper growth and development and protecting it from the attack of foreign pathogens. Other innumerable functions performed by EPS producing microbes constitute shielding from desiccation, protection against stress. PGP bacteria improve plant growth by preventing the proliferation of phytopathogens and thereby support plant growth. Some PGP bacteria synthesize antifungal antibiotics, e.g. *Pseudomonas fluorescens* produces 2,4-diacetyl phloroglucinol which inhibits growth of phytopathogenic fungi. In recent years, fluorescent *Pseudomonas* has been suggested as potential biological control agent due to its ability to colonize rhizosphere and protect plants against a wide range of important agronomic fungal diseases such as black root-rot of tobacco, root-rot of pea, root-rot of wheat, damping-off of sugar beet and as the prospects of genetically manipulating the producer organisms to improve the efficacy of these biocontrol agents

[108-112].

Growth enhancement through enzymatic activity is another mechanism used by plant growth promoting bacteria. Plant growth promoting bacterial strains can produce certain enzymes such as chitinases, dehydrogenase, β -glucanase, lipases, phosphatases, proteases etc. exhibit hyperparasitic activity, attacking pathogens by excreting cell wall hydrolases. Through the activity of these enzymes, plant growth promoting bacteria play a very significant role in plant growth promotion particularly to protect them from biotic and abiotic stresses by suppression of pathogenic fungi including *Botrytis cinerea*, *Sclerotium rolfii*, *Fusarium oxysporum*, *Phytophthora* sp., *Rhizoctonia solani*, and *Pythium ultimum* [113-115].

Effects of soil bacteria on the soil ecosystem

Soil bacteria including different groups along with fungi are able to enhance the availability of different nutrients by utilizing different mechanisms. PGP bacteria are able to enhance the availability of different nutrients including N, P and micronutrients e.g. *Rhizobium* sp., in symbiosis with their legume host plant, and *Azospirillum* in non-symbiotic association with their host plant, can fix atmospheric N_2 [148-153]. PGP bacteria including *Arthrobacter*, *Bacillus* and *Pseudomonas* are able to enhance P availability, by production of organic acids and phosphatase enzymes through producing siderophores, PGP bacteria can also increase Fe solubility and hence uptake by plant [46]. Soil particles are bound by organic chemicals including compounds produced by soil bacteria. A wide range of biochemical is produced by soil bacteria among which polysaccharides are the ones with the highest impact on binding soil particles. The mineralizing effects of soil microbes on organic matter can also influence soil structure. The enhanced growth of plant growth by soil microbes and hence the increased amount of root exudates and rhizo deposition can also affect soil structure directly or by increasing the microbial population and activities, indirectly [154-156].

Soil microbes produce a wide range of biochemical, affecting soil environment. Among which there are the products, adversely affecting the growth and activities of soil pathogens including soil bacteria and soil fungi e.g. PGP bacteria produce hydrogen cyanide (HCN), which can have unfavorable effects on the growth of soil pathogens. In addition through stimulating plant systemic resistance, soil microbes can enhance plant resistance to pathogens. The presence of soil microbes in the rhizosphere and production of different compounds can stimulate plant growth and systemic resistance. Generally, the adverse effects of PGP bacteria, which is mostly related to *Pseudomonas* and *Bacillus* on soil pathogens is through the production of antibiotic compounds (HCN, pyrrolnitrin, phloroglucinols, phenazines, pyoluteorin, and cyclic lipopeptides); plant induced systemic resistance and interfering with pathogens ability to suppress plant growth.

In the recent years there have been some interesting research work regarding the use of PGP bacteria under stress. There are many soil stressors affecting plant growth and yield production including soil pH, suboptimal root zone temperature, and heavy metals. Interestingly, researchers have found that the adverse effects of different stressors on the *Rhizobium*-legume N_2 fixation can be alleviated by the use of signal molecule genistein. Genistein is produced by the specific legume host plant like soybean (*Glycine max* L.) activating the nodulation (nod) genes in *Bradyrhizobium japonicum* [157,158]. Under humid or dry climate conditions soil pH can fluctuate much. The high amounts of rain in the humid area reduce soil pH significantly. PGP bacteria can also alleviate salinity stress on plant growth. They are able to produce the important bacterial enzyme ACC-deaminase under different conditions including stress, which can effectively control the stress. This is because, as previously mentioned, ACC-deaminase can catalyze the ACC, which is the prerequisite for the production of the stress hormone, ethylene. Increased level of ethylene in the plant can adversely affect plant growth and yield production. Plant physiological and morphological characters are also important in the alleviation of stress in symbiosis of non symbiosis association with their associative soil microbes. The more resistant plant species can perform more efficiently under stress and their symbiosis with their associative soil microbes also can intensify such abilities.

Conclusion and Future Prospect

Sustainable agriculture requires the use of strategies to increase or maintain the current rate of food production while reducing damage to the environment and human health. The use of microbial plant growth promoters is an alternative to conventional agricultural technologies. Plant growth-promoting microbe can affect plant growth directly or indirectly. The direct promotion of plant growth by PGP microbes, for the most part, entails providing the plant with a compound that is synthesized by the bacterium or facilitating the uptake of certain nutrients from the environment. The indirect promotion of plant growth occurs when PGP microbes decrease or prevent the deleterious effects of one or more phytopathogenic organisms. The need of today's world is high output yield and enhanced production of the crop as well as fertility of soil to get in an ecofriendly manner. Hence, the research has to be focused on the new concept of rhizo engineering based on favorably partitioning of the exotic biomolecules, which create a unique setting for the interaction between plant and microbes. Future research in rhizosphere biology will rely on the development of molecular and biotechnological approaches to increase our knowledge of rhizosphere biology and to achieve an integrated management of soil microbial populations. The application of multi strain bacterial consortium over single inoculation could be an effective approach for reducing the harmful impact of stress on plant growth.

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