

# Structural and functional diversity of plant growth promoting microbiomes for agricultural sustainability

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## ABSTRACT

The plant allied microbes are phyllospheric, endophytic, and rhizospheric that is allied with plants eco-systems. These microbes have are termed as plant growth promoting (PGP) microbes as they have an ability to enhance growth of plant through indirectly or directly PGP mechanisms. The PGP microbes improve the growth and development of plant under both normal and diverse abiotic stresses conditions of temperatures, pH, salinity and drought. The microbes uses subsequent mechanism to stimulate the plant growth like biological nitrogen fixation; solubilization of minerals (P, K and Zn); production of phyto-hormones (Indole acetic acid, cytokinin and gibberellic acid); 1-aminocyclopropane-1-carboxylate deaminase attributes; production of extracellular hydrolytic enzymes (amylase, cellulase, chitinase, pectinase, protease, and xylanase), siderophores, hydrogen cyanide and ammonia. The PGP microbes sorted out from soil and plant associated are belong to several phylum of all three domain, that is, Archaea, Bacteria and Eukarya with predominant species of genera *Arthrobacter*, *Pseudomonas*, *Aspergillus*, *Bacillus*, *Burkholderia*, *Colletotrichum*, *Exiguobacterium*, *Flavobacterium*, *Fusarium*, *Halobacillus*, *Haloferax*, *Lysinibacillus*, *Paenibacillus*, *Penicillium*, *Psychrobacter*, *Sediminibacillus*, *Streptomyces*, *Trichoderma*, and *Virgibacillus*. In agriculture PGP microbiomes potentiality has increased steadily as it is an effective way to reduce the use of different chemical-based fertilizer, pesticide and other supplements. Present progress on research related to PGP microbial diversity (plant and soil microbiomes), along with their colonizing capability and action's mechanism should increase their applications for plant growth and disease management of agricultural system toward the agricultural sustainability. Present review deals with the structural and functional diversity of PGP microbiomes for agricultural sustainability.

## 1. INTRODUCTION

Globally, the fundamental conservation of world's genetic resources is maintained by the diverse microbial groups. The phyllosphere, endophytic, rhizosphere, and soil are a main hot spot for microbial diversity which is mainly expressed as functions adaptation that help in plant growth and development. In contemporary times, agriculture production is mostly relying upon the chemicals fertilizers to meet the increasing population food demand. Different chemical fertilizers enhanced higher production of crops and heel the related crops problem, but there utilization turns bitter and highly disappointing

consequences. These chemical synthesized fertilizers use in agriculture might deplete the soil fertility, and it becomes acidic and along with all these natural availability of macro and micro minerals may also get depleted. Thus, it is required for awareness timely and to use inputs that are environmental friendly such as plant growth promoting (PGP) microbes and save our "currency" that use in chemical fertilizers and pesticides [1].

PGP soil and phytomicrobiomes practice in agriculture has been proved to facilitate the growth of leguminous and non-leguminous crops and can be a developing strategy. Microbial inputs have many advantages like they are simple to use, inexpensive and have no destructive effect on soil. The main aim of the microbial inputs is, they help in the availing the nutrients to the plants for their better enhancement [2]. During the past few decades, the microbial inoculants have tremendously increased worldwide for agricultural sustainability. Microbial input has repeatedly reported for significant

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increasing in the agronomically important crop yield and growth [3]. PGP soil and plant microbes inhabit diverse niche in agro-ecosystem. The one of the common niches of plant and bacteria for synergism is phyllosphere. Microbes found on the surface of leaf are the stress-adaptive microbes as they tolerate the abiotic stress like high temperature (40–55°C) and UV radiation. *Pseudomonas*, *Pantoea*, *Methylobacterium*, and *Agrobacterium* have been earlier reports as epiphytic microbiomes [4-6]. Microbes found in rhizospheric region have capability to attract toward root and derive maximum benefits from root exudates [7]. Other niche specific microbes are endophytic microbes that reside interiors of the plant, that is, tissues and these microbes are believed for not causing any substantial damage to the host. PGP soil and phytomicrobiome have been reported from different variety of plants such as oilseed rape [8], tomato [9] {Nejad, 2000 #1512; Abbamondi, 2016 #525}, sugarcane [10], sweet corn [11], potato [12], citrus [13], cotton [14], prairie [15], and agronomic plants [16]. *Thermomonospora*, *Streptomyces*, *Pseudomonas*, *Planomonospora*, *Pantoea*, *Nocardioideis*, *Micromonospora*, *Microbiospora*, *Burkholderia*, and *Achromobacter* were isolated and characterized from wheat internal tissue [17,18].

Microbiomes as phytomicrobiome (endophytic-in internal tissues; rhizospheric-rhizospheric zone, and epiphytic- on phyllosphere) have been stated to increase the crop growth under the natural normal and harsh environmental conditions directly by fixing the atmospheric nitrogen, solubilizing soil minerals such as zinc, potassium, and phosphorus, producing low molecular weight plant growth regulators (PGRs), that is, gibberellins (GBs), cytokinin (CK), and auxin (indole acetic acid [IAA]) and siderophores [19,20]. Plant growth is also promoted indirectly by the microbes through producing the substances that have antagonist effect on phytopathogens [21]. As beneficial phytomicrobiomes have an antagonist ability to control phyto-pathogens and provide huge amount of essential minerals so, these beneficial phytomicrobiome could be used as biofertilizer and biopesticides in form of bioinoculants which can be fit for the long term agricultural sustainable system [22]. There are huge number of phytomicrobiome species associated with rhizosphere of plant have been reported belonging to the various genera such as *Serratia*, *Rhizobium*, *Pseudomonas*, *Methylobacterium*, *Flavobacterium*, *Erwinia*, *Enterobacter*, *Burkholderia*, *Paenibacillus*, *Bacillus*, *Acinetobacter*, *Arthrobacter*, *Alcaligenes*, and *Azospirillum* [23].

On the other hand, PGP microbes living in the non-root associated soil have also been recognized for exhibiting multifunctional PGP attributes which may benefits in promoting the plant growth and development [21]. Diverse group of microbes were reported from different soil (normal, acidic, alkaline, nutrient depleted, and saline) which belongs to different genera including *Azospirillum*, *Alkanindiges*, *Bacillus*, *Burkholderia*, *Providencia*, *Mycobacterium*, *Novosphingobium*, *Pseudomonas*, *Paenibacillus*, *Rhodanobacter*, *Sphingomonas*, *Sphingobium*, and *Serratia* [1].

Development of biofertilizer for commercial applications, one of the major challenges is ensuring the effective selection of strain, its screening procedure, so that promising microbial strain is brought forward. In the industries of agricultural chemicals, per annum thousands of prospective compounds are screened and the best compounds are selected which have efficient high throughput assay for further development. On the other hand, similar approaches are not yet applied for the PGP microbes. Effective strategies for initial selection and screening of PGP microbial isolates are required. It may be important to consider specificity or missing N<sub>2</sub>-fixing bacteria from

rice rhizosphere [24]. One approach for organisms selection with the potential of inhibition of soil-borne plant pathogens is to use indigenous microbes [25]. Another approach involves traits-based selection known to be allied with PGP microbes i.e. root colonization [26]. The spermosphere model, a technique of enrichment which relies on the exudates of seed as the source of nutrient has been used for isolation and selection of protease activity [27] and antibiotic [28] and siderophores production [29]. The effective bioassays development and high throughput assay systems facilitate superior strains selection [30].

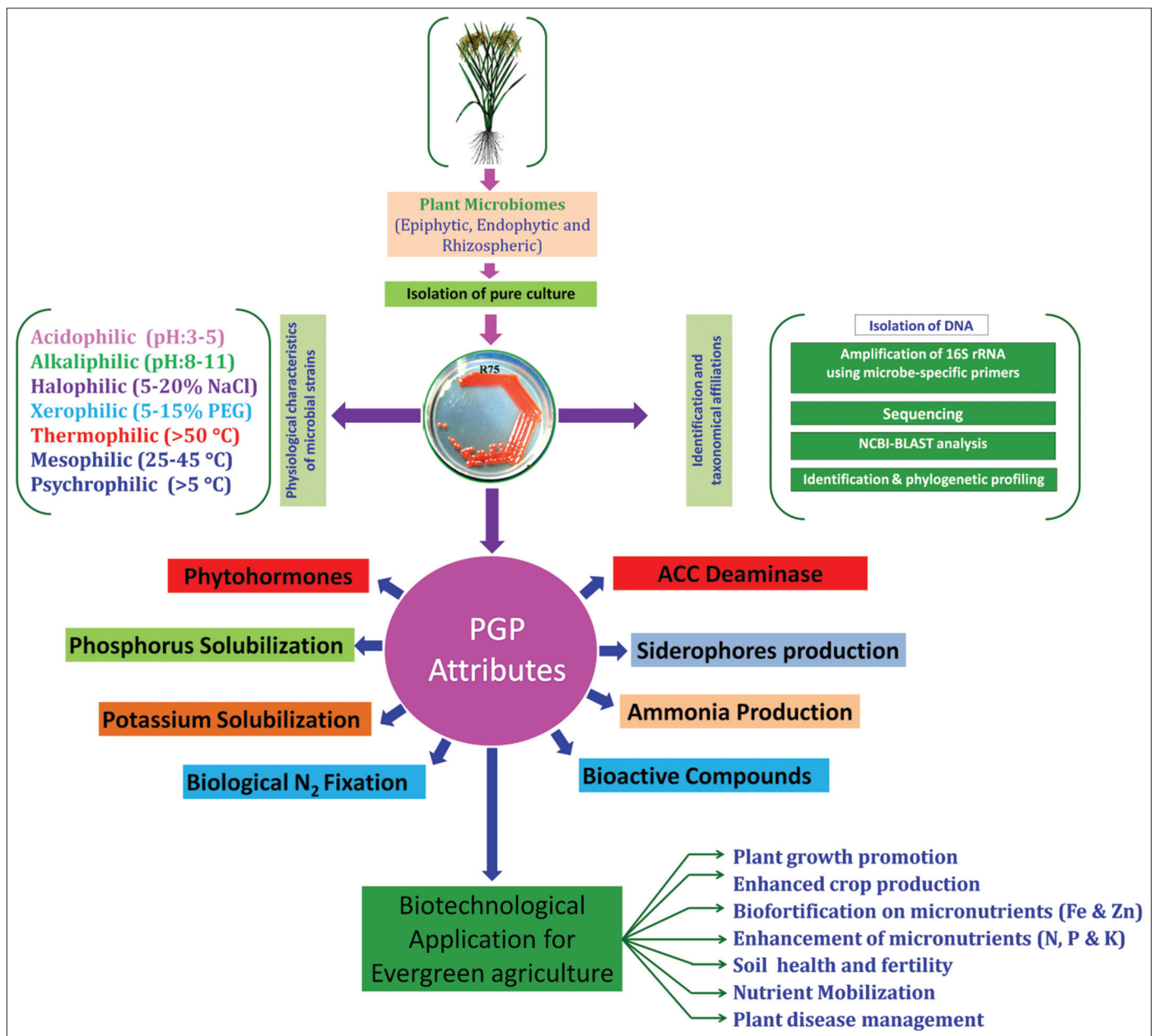
To get a single natural beneficial microbial isolate with multifarious activities of biofertilizers and biocontrol nature is not only difficult but somewhat practically impossible. However, if different beneficial microorganism could be combined as microbial consortium, it would have the desired multifarious activities of biocontrol and biofertilizers nature. PGP soil and phytomicrobiomes will be evaluated in wheat crop for improved nutrient availability, nutrient uptake and nutrient use efficiency. The positive interaction established by the microbes with the plants can play a major role in agriculture as well as environments. The present review describes about the structural and functional diversity of soil and phytomicrobiomes with their potential biotechnological applications for crops improvements and soil fertility.

## 2. BIODIVERSITY OF BENEFICIAL PGP MICROBIOMES

The biodiversity encompasses all life forms, ecological processes and ecosystems and acknowledges the hierarchy at genetic, taxon, and ecosystem levels. Diversity of microbes on other hand comprised of the unicellular algae, bacteria, fungi, protozoan's and constitute the most extraordinary life reservoir in the biosphere, and one which we have only begun to explore. In nature, microbes represent the richest repertoire of both chemical and molecular diversity as they underlie basic processes of ecosystem. At present, the invention of the world's diversity especially microbes is incomplete, and we have a very small idea about the true microbial diversity. About 1.7 million living species of our planet has been identified by the scientists, out of which prokaryotes species are only 5,000 and bacterial species are 1 to 10% known [31]. Millennially, diverse biological materials have yielded by the beneficial soil and plant microbes that are useful to humans such as growth hormones, herbicides, enzymes, drugs and antibiotics. Diversity of soil and phytomicrobiome is the fundamental to survival and economic well-being of human as they are resources reservoir which we can utilize for our benefit. Different beneficial soil and phytomicrobiome are significant for a sustainable biosphere as they performs recycling of nutrients, produces and consume gases that affects the global climate, treat wastes, destroy pollutants [21,32]. The microbial diversity study is also important for solving new and emerging problems of disease and to advance biotechnology. In few words, exploration, evaluation of microbial diversity is essential for industrial, scientific and social development. Biodiversity is an essential ingredient of environment conservation and is central to production of agriculture products [Figure 1].

### 2.1. Structural Diversity

To determine the microbial diversity from different sources and habitats, the traditional method consisted of culturable organism's identification from soil system up to species level and uses the taxonomic differences to measure diversity [33]. However, through this technique only lesser fraction of soil bacterial diversity (1–10%) are culturable [34] and taxonomic differences of isolated strains based on physiological characteristics are also not sufficiently discriminated. To overcome



**Figure 1:** A schematic representation for characterization of microbes and their biotechnological applications for agricultural sustainability. Adapted with permission from Kour *et al.* [89].

these biases induced by cultivability, microbial fatty acid analysis could be utilized to study their diversity [35]. Although, structure of microbial community are enable to be examined through whole soil fatty acid methyl ester analysis [36]. Moreover, phospholipids fatty acid analysis is also enables to estimate the living microbial community structure [37] but provide the information on certain microbial groups, however not permits the detection up to species level [38]. Therefore, direct molecular-based approaches have to be utilized to obtain a wider image of soil bacterial community. Bacterial diversity could also be studied by the cloning and sequencing of the 16S ribosomal DNA of bacteria. The technique, molecular finger printing have then been introduced for the numerous samples simultaneous analysis. Among these techniques, denaturing gel electrophoresis (DGGE), 16S rRNA gene analysis permits finger printing of the dominant bacteria of a given sample [39]. The DGGE patterns represent detectable bacterial

population's relative abundance and could release to the bacterial community biological structure. The simplest bacterial community analyses are based on DNA profile, generated PCR which is followed by restriction digestion of amplification product. Considerable diversity has been reported in cultured form using BIOLOG [40]. 16S rRNA gene sequencing use provides greater discrimination and better characterization of isolates then than earlier studies [41].

## 2.2. Functional Diversity

Microbial diversity could be defined in terms of genetic, taxonomical affiliation and potential functional diversity [42]. In the plant rhizosphere, metabolic versatility in population of microbes is based on its population and genetic variability with other organism (eukaryotic and prokaryotic such as plants) [43]. A putative PGP

microbial strain qualifies as PGP microbiomes when they are able to produce a progressive effect upon inoculation on the plant [44]. The term PGP microbes encompass variety of microbes whose properties and functions favor growth and survival of plant. Several functions may be related to such a beneficial effect such as enhancement of root growth by the phytohormones production, facilitation of water uptake by mucigel secretion (polysaccharides) in zone of root hair. Another function includes improvement of nutrients in plant for example by minerals solubilization like phosphorus, organic mineralization, siderophores secretion for iron nutrition, and associative  $N_2$  fixation [45]. Applications of beneficial PGP microbes in agricultural system are one of the best approaches that play a pivotal role in production of crop, protection and sustained health and fertility of soil [2]. In the past decades, association of PGP soil and plant microbes with different cereals crops including have been identified as *Serratia*, *Pseudomonas*, *Providencia*, *Paenibacillus*, *Methylobacterium*, *Lysinibacillus*, *Kocuria*, *Citricoccus*, *Burkholderia*, *Bacillus*, *Azotobacter*, *Azospirillum*, *Arthrobacter*, and *Acinetobacter* [46,47].

Soil and phytomicrobiomes as promoters of plant growth may either indirectly or directly using diverse PGP mechanisms [Figure 2]. Direct stimulation for growth of plant includes supply of necessary nutrients such as nitrogen, potassium, phosphorus, iron and zinc, by undergoing various mechanisms such as solubilization (P,K, N, Zn), fixation (N) and production (siderophores for the acquisition of iron). PGP microbes also synthesize phytohormones such as auxin, CKs, and GBs and enzymes that also help plants directly in their plant growth. Indirect growth promotion of plant includes inhibiting the phytopathogens (biocontrol) growth through antibiotics, hydrogen cyanide production and siderophores [48,49]. Among microbes, there is root intimacy and proximity gradient as follows: Microbes inhabiting nearby to the roots soil, utilize the metabolites as C and N source that are leaked from the plants roots, microbes colonizing the rhizoplane, microbes living in interiors of the roots tissues, inhabiting spaces between microbes living inside cells cortical and cells in specific structures of nodules, or root. Within this classification, several mechanisms of PGP effects have been established.

### 2.2.1. Direct plant growth promotion

Plant and soil microbiomes as beneficial plant growth promoters have been sorted out to directly facilitate the plant hosts proliferation. They could avail nutrients such as nitrogen (N), potassium (K), phosphorus (P), zinc (Zn) by  $N_2$ -fixation, and solubilization of other nutrients

available in soil as inorganic form; synthesize siderophores that helps in availing the iron (Fe) from the soil by sequestration and solubilization; they synthesize several phytohormones which have ability to enhance the plant growth at various stages; they can also synthesize some less well characterized compounds and enzymes that have low molecular mass which also modulates the plant development and growth [50]. There are number of microbes possess the multifunctional PGP attributes [Figure 3].

#### 2.2.1.1. Mineral solubilization and mobilization

Phosphorus (P) is the second most vital macronutrients after nitrogen and is an essential plant nutrient. This macronutrient present in inorganic form in the soil which is recycled naturally by microbes. Soil and plant microbes are involved in the various processes that transform the soil P and maintain the natural P cycle [51]. Besides the naturally availing of P, huge proportion of soluble form of phosphate is added in the soil for the rapid plant growth but as soon after the addition of the input lowers and it becomes unavailable [46]. The phenomenon of precipitation and fixation of P in soil depends on various factors and one of the factors is soil pH as in the acidic pH, the compounds of Al and Fe phosphate is formed, and if the soil is calcareous than pH get precipitated and compounds won't be formed. Microbes are the major transformer of P even from the poorly available soil pools [52].

Huge number of soil microbes particularly belonging to *Bacillus* and *Pseudomonas*, has a ability to change the insoluble form to soluble of P by secreting various organic acids such as acetic acid, fumaric acid, formic acid, glycolic acid, lactic acid, succinic acid, and propionic acid [53]. The solubilization of P is required because plant only utilizes only organic P and inorganic P that has to be enzyme hydrolyzed known as phosphates, which mostly originate from the plants root through the microbial cation. Since then it has been recognized that there are specific soil microbes groups that enhances the phosphates availability to the plants, not only by organic mineralizing phosphorus compounds but also rendering inorganic phosphorus form of compounds more available to them [54]. Since the last two decades phosphate solubilizing microbes (PSM) has received considerable attention as they have efficacy in dissolving the insoluble phosphates present as rock phosphate, hydroxyapatite and bone meal [55].

PSM includes all the main form of microbes, that is, eukarya, bacteria, and archaea. Amongst bacteria most efficient P solubilizers belongs to different species of *Bacillus* and *Pseudomonas* genera; while among

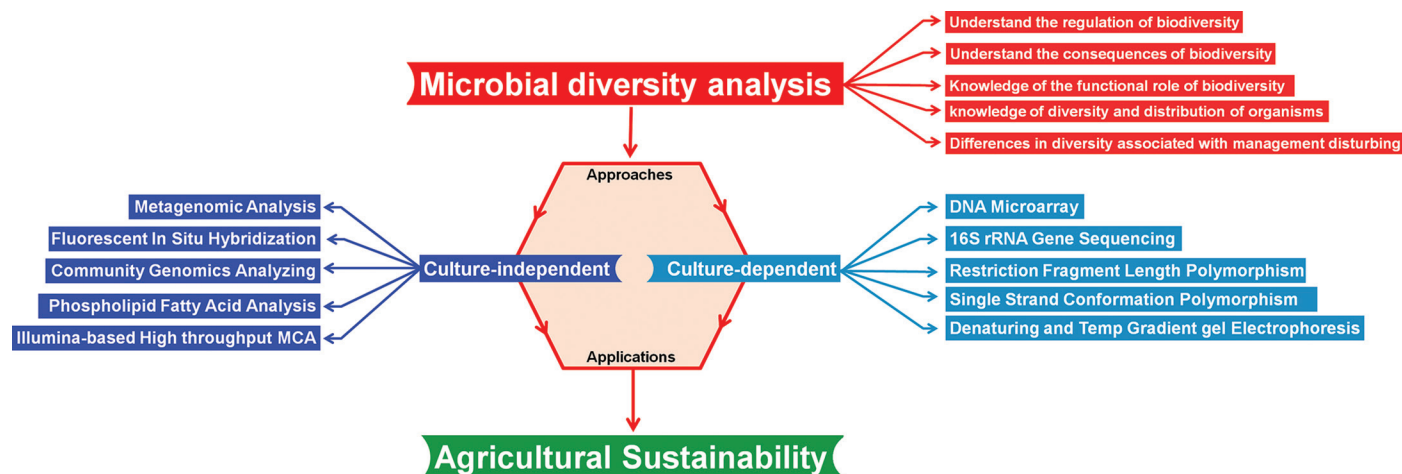


Figure 2: Microbial diversity analysis approaches.



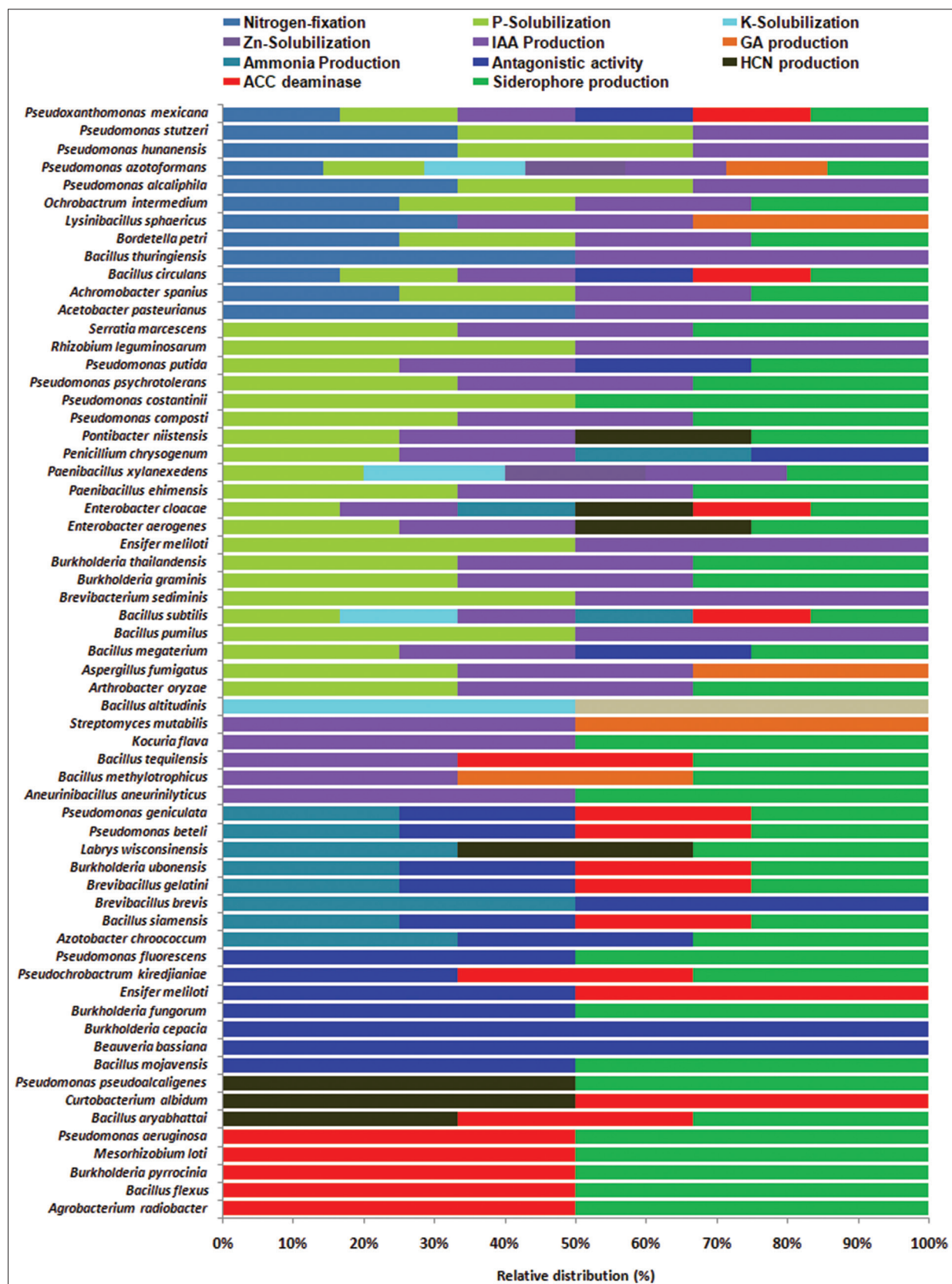


Figure 3: Multifarious plant growth promoting beneficial microbiomes and their relative distribution.

archaea *Natrinema* sp. is most efficient phosphorus solubilizers under the saline conditions [56]. On the other hand, microbes belonging

to eukarya domain were found to *Aspergillus*, *Talaromyces* [57], and *Penicillium* [16]. Microbes directly influences the plant ability

to acquire P from the soil through range of process or structural mediated mechanisms like increasing the surface area, length of root, branching, root hairs [58]. Phosphorus uptake can also be increased by displacing the sorption equilibrium that increases the total transfer of ions of phosphorus (phosphate ions). These mechanism and processes of mineralizing and solubilizing of phosphorus that can be avail and utilized by the plants even from the poorly available both phosphorus form i.e. organic and inorganic forms.

Soil is a habitat for wide variety of microbial species which employ solubilization reaction for the release of soluble P from insoluble form [59,60]. The PGM potential are acknowledged as a efficient P biofertilizer and are utilized as bioinoculants for crops grown in soil amended with insoluble forms like rock or tricalcium phosphate [61]. Inoculation with *P. Bilaji* a potant P solubilizer in wheat plant resulted in greater uptake of Zn, Cu, and Fe [62]. Several species of genera *Xanthomonas* and *Bacillus* that were found to be P solubilizers, which stimulates the physiological parameter and growth of canola (*Brassica napus* L.) however, fails to influence the uptake of P by plant [63]. The study suggested that plant growth and yield is influenced by the phyto-hormones production like IAA by these rhizobacteria. Rhizobia have also been recognized as a solubilizer of organic and inorganic phosphates reported the increase in P-uptake and dry matter of lettuce and maize by inoculation [63].

Organic P is catalyzed by phosphatase or phytase through the hydrolysis of C-O-P ester bonds, which are very significant in the plants nutrition [64,65]. The soil that are low in pH, are rich in organic form of P and after the fungi was tested *Aspergilla* were found to have the maximum activity [64]. These phosphatase producing *Aspergillus* strains when inoculated wheat and chickpea grown in acidic soils of Western Rajasthan (India), resulted in the increased the P uptake biomass and yield [66]. Sawatzki *et al.* [67] reported that 52 fluorescent pseudomonades were sorted out from the forest soil of Western Ghats of Uttar Kannada district solubilized TCP and from TCP the amount of P released ranged from 1.78% to 15.44%, twelve isolates showing high TCP solubilization were recognized as *Pseudomonas fluorescens*, *Pseudomonas poae*, *Pseudomonas trivialis*, and *Pseudomonas* spp. These isolates showed higher solubilization of North Carolina rock phosphate than Mussoorie and Udaipur rock phosphate. In a report, a bacterium, identified as *Burkholderia vietnamiensis* was isolated from the rhizosphere soil associated with ginseng. It was recognized as an efficient solubilizer of phosphorus that was suggested to be developed as biofertilizers [68].

In another study, *Bacillus megaterium* was found to solubilize tricalcium phosphate, which was isolated from rhizospheric plant of native plant from Sichuan of China [69]. In a report, phosphate solubilizing bacteria were sorted out root soil of *Aloe barbadensis*, which were recognized as *Burkholderia gladioli*, *Enterobacter hormaechei*, *Pseudomonas synxantha*, and *Serratia marcescens*. These bacteria were tested on *Aloe barbadensis* as a one consortium and found to enhance the P availability, uptake of P by plant and also increased plant growth [70]. In a study, *Pseudomonas* sp. isolated from soil adhering the roots of *Solanum lycopersicum*, and it was found to be efficient phosphorus solubilizers, along with pesticide tolerant [71]. *Bacillus thuringiensis* was also reported for solubilizing phosphours. In a study this bacterium was also reported to increase the peanut growth grown in acidic soil when inoculated [72]. In another study, thermotolerant bacterium species belonging to genera *Brevibacillus* and *Bacillus* was characterized for the P solubilization, and it was found as an efficient solubilizer of rock phosphate [73].

Fungal species are also well recognized for the solubilization of phosphorus. Fungal species belonging to genera such as *Aspergillus*, *Fusarium*, and *Penicillium* were reported as efficient solubilizer of phosphorus. These strains were isolated from different crops rhizosphere such as haricot beans, faba bean, cabbage, tomato, and sugar cane [74]. *Bacillus cereus* was isolated from rhizosphere Cabbage was also reported for solubilizing phosphorus [75]. In another study, two different fungi isolated from rhizospheric soil of moso bamboo namely, *Aspergillus neoniger* and *Talaromyces aurantiacus* were found to be efficient P solubilizer [57]. *Pseudomonas libanensis* from maize was also reported as a P solubilizer [53]. *Tsukamurella tyrosinosolvens* from tea was also reported as efficient P solubilizer [76].

#### 2.2.1.2. Biological nitrogen fixation (BNF)

Nitrogen (N) is the most needed element for entire living world including microbes, plants and animals. In air, N is abundant as it composes 78% of the earth's atmosphere. Although nitrogen is present in such a huge amount in the air, still it is unavailable to the plants because they cannot use the available form. To avail the nitrogen to plants, it should be transform into ammonia [45]. Nitrogen present in the atmosphere is transformed into forms that can be uptake by plants by following three processes: atmospheric nitrogen conversion into oxides of nitrogen; Industrial fixation of nitrogen uses high range of temperature (300–500°C) and catalysts to form ammonia from nitrogen, whereas microbes uses complex system of enzyme named as nitrogenase to convert nitrogen and ammonia and this process is known as BNF [47,77].

Biologically, about 60% of the nitrogen is fixed by the beneficial nitrogen fixing microbes. BNF represent the economic benefits and can be substitute to chemical fertilizer [78]. Biologically, fixation of atmospheric di-nitrogen is carried by a special enzyme named, nitrogenase coded by *nif* gene which is secreted by fixers of biological nitrogen (free living and symbiotic) [47]. Symbiotic microbes mainly bacteria fixes the N for the leguminous plants like *Rhizobium*, whereas free living nitrogen fixers can also fix N for the non-leguminous plants with a non-obligate interaction with host and these microbes are known as diazotrophs like *Azospirillum* sp. [79]. Genus *Azospirillum* is the one of the efficient and potential diazotrophs that present in bulk soil and it was first isolated from the nitrogen poor soil by Beijerinck [80]. Other PGP microbes that have ability to fix nitrogen are Actinomycetes in non-legume forming trees, and free living N<sub>2</sub>-fixers as *Pseudomonas*, *Klebsiella*, *Bacillus*, blue green algae, *Acetobacter*, and *Azotobacter* [81].

Bacteria from the root endosphere, *Stenotrophomonas* spp., *Bacillus* sp. and *Acetobacter pasteurianus* was reported as efficient nitrogen fixer. They have also reported for the production of phytohormone and help in the significant enhancement of growth parameter and nitrogen content in root as well as shoot [82]. Islam *et al.* [83] reported *Bacillus subtilis*, *Bacillus amyloliquefaciens*, *Pseudomonas stutzeri*, and *Stenotrophomonas maltophilia* for exhibiting acetylene reduction activity and other PGP attributes including production of auxin (IAA) and antagonistic activity against pathogen causing Phytophthora crown rot in cucumber plant. In another report, diverse nitrogen fixing bacteria was reported belonging to genera *Acinetobacter*, *Enterobacter*, *Ensifer*, *Erwinia*, *Klebsiella*, *Pseudomonas*, *Rhizobium*, and *Sinorhizobium* [84]. Xu *et al.* [85] confirmed *Enterobacter oryzae*, *Psychrobacillus psychrodurans*, *Sphingomonas trueperi*, *S. trueperi*, and *S. trueperi* as nitrogen fixers. The inoculation of these strains on the maize and wheat crop has enhanced growth parameter and nutrient content.

In a report, *Paenibacillus* spp. was reported as efficient fixer of nitrogen. This strain was also reported for the production of IAA, and its inoculation in tomato seedlings have positively effects the growth [86]. Rana *et al.* [87] have reported, an endophytic bacterium, *Acinetobacter guillouiae* for fixing nitrogen. The inoculation of this strain on wheat crop has increased growth as well as physiological parameters. In a similar report, endophytic bacteria *Pseudomonas brenneri*, *Pantoea agglomerans*, and *Ewingella americana*, isolated from different cereals crops have reported for fixing nitrogen. There inoculation on the maize crops have significantly increased length of shoot and root, content of chlorophyll, anthocyanin, protein, and physiological availability of iron [88].

#### 2.2.1.3. Production of phytohormones

PGP microbes could also stimulate the growth of plant by producing the phyto-hormones/PGRs [89]. PGRs are organic in nature which influences the plant physiological parameters at much low concentration. PGRs include metabolites of bacteria that aid for plant growth as well as development; examples of PGRs are plant hormones or bioactive compounds produced by PGP microbial strains, such as *Arthrobacter*, *Aspergillus*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Halobacterium*, and *Penicillium*, *Pseudomonas*. PGRs beneficial affect the plant by proliferating and promoting of root system resulting in the efficient uptake of nutrients and water [47]. Tien *et al.* [90] observed production of PGP bioactive compounds by *Azospirillum brasilense*, a nitrogen fixing bacterium in liquid culture. This bacterium was reported to produce small amount of IAA, CK-like and GB substances. Barea *et al.* [91] examined culture supernatant of 50 phosphorus dissolving bacteria for IAA, CKs and GBs sorted out from the rhizospheric region different crop plants. Out of fifty, twenty bacteria were tested positive for the synthesizing all major plant hormones, whereas only IAA producers were 43, 29 were producing GBs and total CK producers were 45. In liquefied culture of *Azospirillum brasilense* Cd, it was observed that the IAA concentration rapidly increases with the stationary phase beginning. These phenomenons suggest that the IAA increase in stationary phase is the overall change of cell metabolic expression when the source of carbon is exhausted [92].

Auxin regulates elongation of root and other plant physiological processes. IAA is the auxin which occurs naturally. Many PGP rhizobacterial strains such as *Azospirillum*, *Bacillus*, and *Pseudomonas* have been known to produce auxin and promote development of root of the plants. The root growth promoter, auxin is synthesized by tryptophan which is an amino acid of root exudates. In exudates the tryptophan concentration varies among the different plants. Although to measure the concentration of produces IAA by microbes is easy in the laboratories but to determine and assess the IAA level in the rhizosphere is difficult as the IAA gene expression is controlled by the both environment and genetic factors. Moreover, in bacteria, it was identified that there are five different methods for the IAA biosynthesis. Seed inoculation with IAA producing *P. fluorescens* WCS 365 did not results the shoot or root weight increase of the sweet pepper, cucumber and tomato, but significantly increases the radish root weight, that produces tryptophan nine times more in its root exudates per seedling [93].

Promotion of plant growth through bacteria is a complex phenomenon, and it is well-established [94]. Plant enhancement is succeeding by the various PGP traits which is exhibited by many bacteria which are associated with plant. Vessey [95] also reported that, PGP microbes that produce IAA increase the roots length and growth, by which the plant access more nutrients from the soil. IAA and related

compound presence could be demonstrated for many diazotrophs such as *Polymyxa* sp., *Paenibacillus*, *Azotobacter*, *Azospirillum*, and *Acetobacter diazotrophicus* [96].

In a study, IAA concentration in the indigenous *Azotobacter* and fluorescent *Pseudomonads* isolates was evaluated in the tryptophan presence and absence [97]. In a report, Pothier *et al.* [98] describes the *Azospirillum* strain interaction with cereal crop roots by applying an approach, that is, DFI- differential fluorescence induction promoter. This approach identifies genes of *Azospirillum brasilense* Sp-245 that were induced in the presence of seeds extract of spring wheat. Microscopic analysis interaction between plant soil bacterium using auto fluorescent proteins are used to elucidate the functioning and establishment of PGP phytomicrobiome in roots [99]. Production of PGRs, IAA and other attributes such as solubilization of P, production of  $\text{NH}_3$  and hydrogen cyanide (HCN) by three nonrhizobial PGP bacteria *Bacillus thuringiensis*, *Enterobacter asburiae*, and *Serratia marcescens* from surface sterilized nodules of Kudzu was studied under *in vitro* conditions by Selvakumar *et al.* [100]. PGP microbial strains promote *Brassicca juncea* growth under chromium stress by producing siderophores and IAA [101]. Verma *et al.* [102], attempted to characterize promising isolates of *Azospirillum*, *Bacillus*, *Pseudomonas* spp. on the IAA production basis which could increase plant growth and yield.

#### 2.2.2. In-direct plant growth promotion

Plants pathogens are major destroyer of the crop under the harsh as well as normal environmental conditions. They can reduce the yield of the crop from 25% to 100%. Biocontrol of phytopathogens has been recognized as an integral component. Microbial genera such as *Burkholderia*, *Bacillus*, *Pseudomonas*, *Streptomyces*, and *Trichoderma* have been reported as the most dominant PGP microbes associated with plant [103]. Such phytomicrobiome can limits the plant damage by controlling the phytopathogens attack by producing certain compounds such as ammonia, antibiotics, enzymes, HCN, siderophores, and volatile compounds (Table 2). These also could function as pathogen competitors for nutrient and sites colonization or as inducers of systematic resistance.

##### 2.2.2.1. Production of siderophores

Iron (Fe), a micronutrient is a necessary nutrient required for the crops growth; however in soil, it is relatively insoluble and is extremely limiting in the plant rhizospheric region [104]. Plant root absorb iron in the reduced form of ferrous ( $\text{Fe}^{2+}$ ) ion and in soil ferric ( $\text{Fe}^{3+}$ ) ion is more commonly available in soil which is well aerated although it is easily precipitated in the iron-oxide form. Plants are commonly known to excrete Fe-chelators that bind to  $\text{Fe}^{3+}$  and help to maintain it in solution. Iron-chelators deliver the  $\text{Fe}^{3+}$  to the plant root surface where it is reduced to  $\text{Fe}^{2+}$  and immediately absorbed. The concentration of Fe is rather insufficient and low for microbial growth. To survive in iron limiting conditions, microbes secrete a siderophores, a Fe-binding ligands which have high affinity ( $K_D = 10^{-20}$  to  $10^{-50}$ ) for the sequestration of Fe from the bulk soil [105]. Siderophores production is beneficial for plants as chelating Fe formerly unavailable. This chelating compound has also some properties of biocontrol as it helps particular microbes to effectively compete against other competing organisms for Fe, especially pathogenic fungi [106]. Siderophores are  $\text{Fe}^{3+}$  specific ligands of low molecular weight. Therefore, through siderophores secretion and production, PGP phytomicrobiome can prevent the phytopathogens proliferation and thereby facilitate the growth of plants. The secreted siderophores molecules find available  $\text{Fe}^{3+}$  from the rhizospheric region and results in the prevention of



any pathogens in its immediate vicinity from proliferating due to Fe deficiency. It should be noted that this mechanism of microbes do affects the plant by iron depletion as plants are capable to require iron at considerably lower concentration (~1000 fold) than microbial pathogens [107].

Kloepper *et al.* [108], firstly demonstrated the siderophores production importance as a mechanism of the improvement of plant growth and biocontrol of phytopathogens. They demonstrated the siderophores mediated antagonism by PGP fluorescent *Pseudomonas* strains against *Erwinia carotovora* increases the crop productivity in the case of potato, radish and sugarbeet. *Pseudomonads* produced yellow-green fluorescent water soluble siderophores (phenolate and hydroxamate) [107]. These siderophores have been classified into 2 main types, pyoverdins and pyochelins [109]. A third siderophores type known as fluorebactin has been sorted out from *P. fluorescens* WCS374 [110]. Apart from *Pseudomonas*, other microbial group such as Archaea, *Agrobacterium*, *Bacillus*, and *Rhizobium*, also produce a different types of Fe-chelating compounds and various plants are capable of Fe chelated using bacterial Fe-siderophores complexes [49].

#### 2.2.2.2. Antagonism

Antibiosis, competition, and exploitation are three classical antagonism categories as antibiosis is the metabolic agents produced by the microbes which have lethal damaging effects, and it is the most effective indirect mechanism of PGP soil and phyto-microbiomes [111]. Antibiotic synthesis by PGP microbes can prevent the proliferation of countless pathogens of plants and thereby this process enhances the plant growth. Number of antibiotics has been identified that was produced by *Pseudomonas* like 2,4-diacetylphloroglucinol (DAPG), tensin, tropone, phenazine, pyoluteorin, pyrrolnitrin, oomycin A, hydrogen cyanide (HCN), cyclic lipopeptide, and amphisin. Compounds produced by the genus *Bacillus*, *Streptomyces*, *Sporosarcina*, and *Stenotrophomonas* have also been identified as Oligomycin A, Kanosamine, Xanthobaccin and Zwrittermicin A [112]. When antibiotic negative mutants were inoculated in the rhizosphere, it does not affects the target organism as did the parent antibiotic producer. It is a good indication that antibiotic is a major factor and several soil born disease can be controlled by seed application of effective PGP microbes. The other category of antagonism is competition. It is the immediate demand of material or conditions and exploitation [113]. Causal mechanism clarification gave new urges to search means for the utilization of biological way to plant protect roots against the pathogens cation through the beneficial soil and phyto-microbiome agency other than the host. During the past 20 years, numerous soil and phyto-microbiomes are able of providing control on disease in the field have been reported worldwide [114].

Several genera of bacteria have shown their biocontrol capabilities both under *in vivo* and *in vitro* conditions such as *Aeromonas* [37], *Arthrobacter* [115], *Azotobacter* [116,117], *Bacillus* [118], *Bradyrhizobium* [119], *Burkholderia* [120], *Enterobacter* [121], *Exiguobacterium* [49], *Paenibacillus* [122], *Pseudomonas* [37], *Rhizobium* [123,124], *Sanguibacter* [37], *Serratia* [125,126], and *Stenotrophomonas* [127] were found to be an effective suppresser of soil-borne fungal pathogens. In fields conditions also, many biocontrol agents exhibited their effectiveness. The different response of PGP soil and plant microbes on different crops is given in Table 1.

#### 2.2.2.3. Aminocyclopropane-1-carboxylate deaminase

Ethylene is a gaseous substance for the growth of plant that has been shown to be vital in many aspects of development and their

response to stress by the plant [128]. In plants, this phytohormone plays an important role in various processes for the development like fruit ripening, epinasty, leaf abscission and leaf senescence [129]. An enzyme known as 1-aminocyclopropane-1-carboxylate synthase (ACC synthase) acts as catalyst that catalyses the first step of the synthesis of ethylene which is irreversible. In this step adenosyl methionine is converted to ACC. The last step in the ethylene synthesis involves formation of ethylene via ACC oxidase from ACC. ACC deaminase hydrolyses ACC, the immediate biosynthetic ethylene precursor in plant and thus plants development and growth are modified. Bacterial strains containing ACC deaminase sequester the ethylene precursor ACC for hydroxylation via ACC deaminase [130]. It has been postulated that different genes subset encoding ACC synthase are expresses in response to various environmental, developmental and hormonal signals [129]. At this time the genes role in ACC synthase encoding, in response to PGP microbe invasion, remains unclear. Ethylene production increases as a result of plant infection by *Rhizobium* and *Bradyrhizobium* [131]. PGP microbial strain, *Pseudomonas putida* GR12-2 is known to cause ethylene level enhancement. A proposed mechanism which stimulates the production ethylene included bacterial synthesis of indole-3 acetic acid [132].

Plant growth enhancing microbes, *Bacillus iodinum*, *Brevibacterium iodinum* and *Zhihengliuella alba* reduced the ethylene concentration, alleviates the salt stress and promotes the growth of red pepper [133]. In another report, PGP phyto-microbe, *Achromobacter xylosoxidans* from rhizosphere *Ocimum sanctum* was found to be potential ACC deaminase activity. This strain enhanced the plant growth of *Ocimum sanctum* grown under waterlogging stress conditions and also it reduces the ethylene concentration [134]. In similar report, *P. putida* was reported to exhibit ACC deaminase activity and inoculation this strain in *Agaricus bisporus* enhanced its growth and relieved the inhibition of ethylene [135]. Another bacterial species of *Pseudomonas*, that is, *P. fluorescens* was also reported to exhibits ACC deaminase activity [136]. ACC deaminase containing rhizobacteria *Arthrobacter protophormiae* was inoculated in *Pisum sativum* grown in salt stress, and it resulted into plant growth promotion and reduction of ethylene damage [137]. *Aneurinibacillus aneurinilyticus* and *Paenibacillus* sp. was found to be ACC deaminase activity *in vitro*. The inoculation of both strains as consortium in French beans grown in salinity conditions were found to enhance biomass, total chlorophyll content and plant growth promotion [138].

### 3. BENEFICIAL MICROBES FOR MITIGATION OF ABIOTIC STRESSES

Microbes are the pioneer colonizer of the earth planet. Microbes are found in all the extreme habitats of temperature, pH, water and salt stress. The “deep hot biosphere” has been recognized due to unique microbial- animal assemblages and nutrient dynamics. It point out the microbial importance and versatility in sustaining the life. The microbes play enormous role in agriculture, environment, industry and medicine because of their remarkable inherent functional and physiological diversity. Very well recognized and commercially exploited microbial activities are supplementation, augmentation and recycling nutrients of plant, which play a major role in agricultural sustainability [138]. In agriculture, productivity and production of crop is inhibited by different environmental stresses including biotic and abiotic [140]. These stresses include flooding, drought, temperature extremes, high light, toxic metal and organic contaminants



**Table 1:** Direct plant growth promoting response of beneficial microbiomes.

Microbes	Host	Response	References
<i>Microbacterium</i> FS-01	Apple	Yield/growth and nutrition	Karlidag <i>et al.</i> [168]
<i>Streptomyces acidiscabies</i> E13	Cowpea	Growth	Dimkpa <i>et al.</i> [169]
<i>Flavobacterium psychrophilum</i> HHS2-37	Wheat	Growth and cold stress	Verma [170]
<i>Achromobacter piechaudii</i> HHS1-31	Wheat	Growth and yield	Verma <i>et al.</i> [171]
<i>Agrobacterium larrymoorei</i> IARI-PC4-102	Maize	Growth and yield	Marag <i>et al.</i> [172]
<i>Methylobacterium phyllosphaerae</i> HHS2-67	Wheat	Growth cold stress	Verma <i>et al.</i> [173]
<i>Pseudomonas fluorescens</i> R-93	Maize	Growth and yield	Gholami <i>et al.</i> [174]
<i>Pseudomonas fluorescens</i> CB-501	Maize	Growth and yield	Fankem <i>et al.</i> [175]
<i>Pseudomonas gessardii</i> IARI-ABR-45	Wheat	Growth and yield	Yadav <i>et al.</i> [176]
<i>Pseudomonas putida</i> RS-198	Cotton	Cotton germination	Yao <i>et al.</i> [177]
<i>Pseudomonas libanensis</i> EU-LWNA-33	Maize	Growth, <i>P</i> uptake	Kour <i>et al.</i> [53]
<i>Pantoea cyripedii</i> IARI-PC4-37	Maize	Growth and yield	Marag <i>et al.</i> [172]
<i>Providencia rustigianii</i> IARI-R-91	Wheat	Growth and yield	Yadav <i>et al.</i> [178]
<i>Pseudomonas cedrina</i> IARI-R-53	Wheat	Growth and yield	Yadav <i>et al.</i> [178]
<i>Nitrincola lacsaponensis</i> SL-11	Wheat	Growth Salt stress	Tiwari <i>et al.</i> [179]
<i>Bacillus amyloliquefaciens</i> HHS2-30	Wheat	Germination and seedling	Verma <i>et al.</i> [180]
<i>Bacillus aryabhattai</i> IARI-PC4-6	Maize	Growth and yield	Marag <i>et al.</i> [172]
<i>Bacillus pumilus</i> SF3-8	Sunflower	Growth	Forchetti <i>et al.</i> [181]
<i>Bacillus subtilis</i> CAS-15	Pepper	Growth and yield	Yu <i>et al.</i> [182]
<i>Exiguobacterium antarcticum</i> HHS2-49	Wheat	Growth and yield	Verma <i>et al.</i> [171]
<i>Paenibacillus tylopili</i> IARI-ABR-36	Wheat	Growth and yield	Yadav <i>et al.</i> [178]
<i>Metarhizium anisopliae</i> LHL07	soybean	Growth and salt stress	Khan <i>et al.</i> [183]
<i>Penicillium citrinum</i> IR-3-3	Rice	Growth	Khan <i>et al.</i> [184]
<i>Penicillium simplicissimum</i> CEF-818	Cotton	Biocontrol	Yuan <i>et al.</i> [185]
<i>Trichoderma harzianum</i> Rani Th-14	Wheat	Growth and drought stress	Rawat <i>et al.</i> [186]
<i>Trichoderma longibrachiatum</i> T6	Wheat	Seedling, salt stress	Zhang <i>et al.</i> [187]
<i>Streptomyces laurentii</i> EU-LWT <sub>3</sub> -69	Maize	Biomass and <i>P</i> content	Kour <i>et al.</i> [16]
<i>Acinetobacter calcoaceticus</i> EU- LRNA-72	Maize	Biomass and <i>P</i> content	Kour <i>et al.</i> [52]
<i>Bacillus cereus</i> AS4	Wheat	Growth and yield	Sezen <i>et al.</i> [188]
<i>Azotobacter chroococcum</i>	<i>Dodonaea</i>	Improved seedlings growth	Yousefi <i>et al.</i> [189]
<i>Hartmannibacter diazotrophicus</i>	Alfalfa	Improved seedling growth	Ansari <i>et al.</i> [190]

presence in the soil, radiation, high salt, wounding, insect predation, and various phytopathogens including fungi, bacteria, viruses and nematodes [141,142]. To overcome the environmental stresses, the plants have the ability to modify its physiology and metabolism including defensive proteins synthesis. In addition, presence of certain rhizospheric bacteria can help the plants to overcome or avoid the several environmental stresses.

The beneficial soil microbiomes with efficient PGP attributes could be used for ameliorate of abiotic stress in plants like alkaline/acidic, high/low temperatures, drought and saline environments. There are huge numbers of finding showing that soil and phytomicrobiomes with multifarious PGP attributes play significant role in mitigation of abiotic stress. In a study of Sandhya *et al.* [143], beneficial microbes belonging to genera *Pseudomonas* namely, *Pseudomonas entomophila*, *P. putida*, *P. stutzeri*, *Pseudomonas syringae*, and *Pseudomonas* spp. were reported as drought tolerant bacteria. The inoculation of these strains on maize seedling growing under water fed conditions were enhancing plant biomass, relative water content, leaf

water potential and decreases leaf water loss as compare to control. Among all the species of the *Pseudomonas*, this study has concluded that *Pseudomonas* spp. was most efficient drought tolerant strain then other. This strain was also reported for lowering the antioxidants enzymes like ascorbate peroxidase (APX), catalase (CAT), and glutathione peroxidase under drought conditions as compare to other stains and uninoculated seedlings. In another investigation, thermotolerant PGP bacterium, *P. putida* have been reported to alleviate the heat stress of wheat plant. Bacterium inoculation also enhanced biomass, length of root and shoot, grains formation, amino acid, chlorophyll, proteins and sugars and on other hand it reduces the antioxidant enzymes concentration such as APX, CAT and superoxide dismutase (SOD) [144].

In an investigation, three PGP rhizobacteria namely, *Brevibacterium casei*, *Brachy bacterium saurashtrense*, and *Haerero halobacter* were reported as efficient strains for alleviating the salinity stress. The inoculation of these strains in *Arachis hypogaea* plant, grown under the saline conditions, enhanced the content of amino acid,

**Table 2:** Indirect plant growth promoting response of beneficial microbiomes.

Microbes	Host	Response	References
<i>Alcaligenes faecalis</i>	Rice	Exhibit ACC deaminase activity and promotes plant growth of rice under salt stress	Bal <i>et al.</i> [191]
<i>Aneurinibacillus aneurinilyticus</i>	Garlic	Promotes plant growth French bean, exhibit ACC deaminase activity and alleviates drought and salinity	Yadav [20]
<i>Azospirillum brasilense</i>	Sugarcane	Production of siderophores	Delaporte-Quintana <i>et al.</i> [192]
<i>Bacillus atrophaeus</i>	<i>Lycium barbarum</i>	Produces antimicrobial secondary metabolites	Ma <i>et al.</i> [193]
<i>Bacillus licheniformis</i>	Soil	Produce hydrolytic enzymes, ammonia and exhibit ACC deaminase activity	Siddikee <i>et al.</i> [194]
<i>Bacillus mojavensis</i>	Soybean	Biocontrol of <i>Rhizoctonia solani</i>	Prajakta <i>et al.</i> [195]
<i>Bacillus stratosphericus</i>	Soil	Produce hydrolytic enzymes, ammonia and exhibit ACC deaminase activity	Siddikee <i>et al.</i> [194]
<i>Bacillus subtilis</i>	Sugarcane	Antagonist against <i>Colletotrichum falcatum</i>	Hassan <i>et al.</i> [196]
	Tomato	Produce siderophores and exhibit ACC deaminase activity	Xu <i>et al.</i> [197]
<i>Bacillus velezensis</i>	Olive	Antagonist activity against <i>Verticillium dahliae</i>	Cheffi Azabou <i>et al.</i> [198]
<i>Beauveria bassiana</i>	Groundnut	Biocontrol leafminer and collar rot disease in groundnut	Senthilraja <i>et al.</i> [199]
<i>Brevibacterium epidermidis</i>	Soil	Produce hydrolytic enzymes, ammonia and exhibit ACC deaminase activity	Siddikee <i>et al.</i> [193]
<i>Brevibacterium iodinum</i>	Soil	Produce hydrolytic enzymes, ammonia and exhibit ACC deaminase activity	Siddikee <i>et al.</i> [194]
<i>Burkholderia cenocepacia</i>	Rice	Production of siderophores	Loaces <i>et al.</i> [200]
<i>Gluconacetobacter diazotrophicus</i>	Sugarcane	Production of siderophores	Delaporte-Quintana <i>et al.</i> [192]
<i>Microbacterium paraoxydans</i>	Rice	Exhibits ACC deaminase activity and produce IAA	Bal <i>et al.</i> [201]
<i>Ochrobacterum intermedium</i>	Sugarcane	Antagonist against <i>Colletotrichum falcatum</i>	Hassan <i>et al.</i> [196]
<i>Paenibacillus elgii</i>	Rice	Exhibits ACC deaminase activity	Bal <i>et al.</i> [201]
<i>Paenibacillus riograndensis</i>	Wheat	Antagonist activity against <i>Burkholderia cepacia</i>	Bach <i>et al.</i> [202]
<i>Paenibacillus xylanexedens</i>	Date palm	Exhibits ACC deaminase activity and produce IAA	Yaish <i>et al.</i> [203]
<i>Pantoea agglomerans</i>	Rapeseed	Production of siderophores, IAA and ACC deaminase	Zhang <i>et al.</i> [204]
<i>Pseudochrobactrum kiredjianiae</i>	Soil	Biocontrol of <i>Rhizoctonia cerealis</i> , <i>Fusarium graminearum</i> , <i>Magnaporthe grisea</i> , <i>Fusarium oxysporum</i> and <i>Botrytis cinerea</i>	Qin <i>et al.</i> [205]
<i>Pseudomonas oryziphobans</i>	Rice	Production of siderophores	Loaces <i>et al.</i> [200]
<i>Pseudomonas putida</i>	Sugarcane	Antagonist against <i>Colletotrichum falcatum</i>	Hassan <i>et al.</i> [196]
<i>Pseudomonas stutzeri</i>	Cucumber	Acetylene reduction activity, biocontrol <i>Phytophthora capsici</i>	Islam <i>et al.</i> [83]
<i>Pseudomonas thivervalensis</i>	Rapeseed	Production of siderophores, IAA and ACC deaminase	Zhang <i>et al.</i> [204]
<i>Serratia nematodiphila</i>	Forest soil	Promotes plant growth of black pepper; produce siderophores and HCN	Dastager <i>et al.</i> [206]
<i>Stenotrophomonas maltophilia</i>	Sugarcane	Antagonist against <i>Colletotrichum falcatum</i>	Hassan <i>et al.</i> [196]
	Cucumber	Acetylene reduction activity, biocontrol <i>Phytophthora capsici</i>	Islam <i>et al.</i> [83]
<i>Streptomyces corchorusii</i>	Rice	Production of hydrolytic enzymes and siderophores	Tamreihao <i>et al.</i> [207]
<i>Streptomyces mutabilis</i>	Soil	Biocontrol of <i>Fusarium culmorum</i>	Toumatia <i>et al.</i> [208]

ACC: 1-aminocyclopropane-1-carboxylate, IAA: Indole acetic acid, HCN: Hydrogen cyanide

phosphorus and nitrogen as compare to control [145]. Cold stress is also a one of major suppressors of the PGP and its alleviation is also reported by the microbes. In a report, PGPrhizobacteria, *Azospirillum brasilense*, *B. megaterium*, *B. subtilis*, and *Raoultella terrigena* along with boron have reported to increase the wheat and barley growth of grown under low temperature stress. The report also concluded that inoculum inoculation lowers the antioxidant enzymes activities including CAT, peroxidase, and SOD and reactive oxygen species was also lowered [146]. Another abiotic stress i.e. acidity is also reported to be beneficial

PGP microbes. In a study, low pH was alleviated in rice plant by the phosphorus solubilizing bacteria *Burkholderia seminalis*, *Burkholderia thailandensis*, and *Sphingomonas pituitosa*. These strains were also reported to improve the growth of the rice plant better in comparison with uninoculated control [147]. Another investigation has concluded that two species of *Bacillus* i.e. *B. subtilis*, and *B. megaterium* from rhizosphere of barley, alleviated the salinity stress and increased the growth of barley. The inoculum of these bacteria improves the roots and shoots length as well as germination percentage [148].

Two *Pseudomonas* species i.e. *P. libanensis* and *Pseudomonas reactans* were found to be efficient strains which are highly resistant to drought, heavy metals, salinity as well as extreme temperature. There inoculation in plant *Brassica oxyrrhina* reported to enhance to growth of the plant as it have a ability to produce indole-3-acetic acid, siderophores and ACC [149]. In a similar report, *Aneurinibacillus aneurinilyticus*, *Alcaligenes* spp, *Bacillus* spp, and *Proteus* sp. sorted out from the *Commiphora wightii* rhizosphere growing in a desert region. These strains were reported to tolerant drought, salinity and high temperature stress. The inoculation of these strains in chilli under both drought and saline conditions enhanced the root as well as shoot length [150]. In another investigation, PGPR *P. putida* and *Novosphingobium* sp. were reported to mitigate the salinity stress in citrus plants. Among both the strains, the study concluded that *Novosphingobium* sp. was an efficient strain as this strain improves the plant growth by lowering the abscisic acid and salicylic acid more [151]. In another study it was reported an arbuscular mycorrhizal fungus, *Funneliformis mosseae* as efficient alleviator of both alkalinity-salinity stresses in watermelon. The inoculations of fungi have also reported for increasing the expression level of antioxidant responses like SOD, APX, CAT and glutathione reductase [152]. Rhizobacterium phosphorus solubilizing microbes *Acinetobacter calcoaceticus* and *Penicillium* sp. were also reported for mitigate drought stress in foxtail millet and improves the accumulation of glycine betaine, sugars and decreases the lipid peroxidation [52]. In another investigation psychrotrophic bacterium, *Glutamicibacter arilaitensis* isolated from night-soil compost. This bacterium was stated to stimulate the growth of plant growing under low temperature conditions [153] [Table 3].

#### 4. RELATIONSHIPS IN BENEFICIAL MICROBIOMES AND ENVIRONMENT

The structure of rhizobacterial community is dynamic as it is influenced by diverse factors like age of plant, the inoculant type (fertilizer inputs). The community shifts during the crop growth results in the pattern modification of root exudation. The PGP microbiome from both plant and soil as a bioinoculants in the form of seed coating or near to the seed in the soil may change the composition of microbial community to either high or small magnitude. The discovery of free living nitrogen fixing bacterial species, that is, *Azospirillum* and *Azotobacter* are also applicable for as agricultural input because they have ability to enhance the crops growth and productivity along with the other microbes management that are pathogens in nature.

The change in traditional crop cultivation and extensive use of chemically synthesized agricultural inputs has resulted in the soil health deterioration physically, chemically and biologically. Therefore, variety of agricultural commodities production, under condition of shrinking resources of land and diminution of both soil biological potential and wealth need to be enhanced. The use of soil microbes that enhance the plant growth will be a superior approach for management of nutrient. The soil microbe's diversity and their activity varies according to their habitat as microbes living in the association of root soil are more diversified and have more number of activities to enhance the growth of crops than microbes living the bulk soil [154]. The root exudates release and plant material decaying provides carbon and energy sources for the beneficial microbiomes associated with root while, activity of microbes is affected by rooting patterns and quantity and quality of root exudates which is modified by the supply of available nutrients to plants [155].

Microbes that establish inside the plant roots are known as endophytes forms more intimate associations. These organisms include a different soil bacterial species forming less formal association than the symbiotic (rhizobia-legume symbiosis) [156]. Endophytic microbes could be sorted out from plant tissues that are surfaced sterilized [157]. In general, endophytes are PGP microbiome in greater proportion than is the case for rhizoplane or rhizosphere inhabiting bacteria [158]. Root nodulating are also endophytic microbes, living in specially developed organs of the root and have ability to promote plant growth through  $N_2$ -fixation [47,159].

Soil bacterial genera *Sinorhizobium*, *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium*, *Azorhizobium*, and *Allorhizobium*, belonging to the Rhizobiaceae family, are associated with roots ecosystem of plants and have capability to form root nodules [160]. Collectively these all bacteria are oftenly referred as rhizobia. The main mechanism by these nodule formatting bacteria improves growth of plant is nitrogen fixation. There are various bacterial strains that have not ability to form nodule in plants, but still increase the plant growth through a multiple mechanisms; these include genera such as *Agrobacterium*, *Arthrobacter*, *Bacillus*, *Caulobacter*, *Chromobacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, and free-living nitrogen-fixing bacteria [161].

In agriculture, PGP microbes including, endophytic bacteria like rhizobia or other root bacteria have been increasingly utilized for crop production over the course of 20<sup>th</sup> century. It is well characterized that plant-bacterial associations, other than the nitrogen fixing systems, can have pronounced effects on the plant growth. These may be manifested through accelerated development and growth due to growth stimulating PGRs production, enhanced minerals availability like Fe, through bacterial siderophores production, or phosphorous through enhanced solubilization [46]; or increased resistance to abiotic stresses like frost damage and/or pathogens [162]. More recently, Glick *et al.* [163] have shown that some PGP microbes that can improve growth of the plant by modulating the plant signals (ethylene) levels.

It is generally presumed that PGP microbes stimulating of plant growth may requires the bacterium which binding to the root of the plant. PGP microbes inoculants or rhizobia use is successful in agriculture either depends upon the viable bacteria delivery to the root zone which is accomplished by inoculation in seeds with a dormant bacterial cells preparation, bulk inoculants or coated seed means. PGP phytomicrobiome have a beneficial effect on growth of host plant *via* an improvement in the status of nutrient, and an intimate relationship between host and the PGP microbiomes. However, the degree of intimacy between PGP microbiomes and the host could differ depending upon how and which part of the host plant, the PGP microbiomes colonizes. Relationships between PGP soil and phyto-microbiomes and the host could be categorized into two complexity levels i.e. rhizosphere and endophytes. In rhizospheric relationships, surfaces of root or even plant superficial intercellular spaces are colonized by the PGP microbiomes. Not any soil bacteria could colonize these areas. By definition, the plant changes the physically and chemically soil composition in the rhizospheric region of plant as compared to the bulk soil that could affect the PGP microbiomes ability to colonize. These alterations are manifested by changes in soil pH, partial pressure of  $O_2$ , water potential, and a myriad of other chemical and physical characteristics due to plant exudations [164-167].



**Table 3:** Beneficial microbes with potential PGP attributes for mitigation of diverse abiotic stress in plants.

Microbes	Crop inoculated	Stress ameliorated	References
<i>Funneliformis mosseae</i>	Watermelon	Alkalinity-salinity	Ye <i>et al.</i> [152]
<i>Bacillus amyloliquefaciens</i>	Wheat	Cold stress	Verma <i>et al.</i> [209]
<i>B. megaterium</i>	Wheat	Cold stress	Turan <i>et al.</i> [210]
<i>Exiguobacterium acetylicum</i>	Pea	Cold stress	Selvakumar <i>et al.</i> [211]
<i>Pantoea dispersa</i>	Wheat	Cold stress	Selvakumar <i>et al.</i> [212]
<i>Pseudochrobactrum kiredjianiae</i>	Wheat	Cold stress	Qin <i>et al.</i> [205]
<i>Pseudomonas lurida</i>	Wheat	Cold stress	Selvakumar <i>et al.</i> [213]
<i>Pseudomonas vancouverensis</i>	Wheat	Cold stress	Mishra <i>et al.</i> [214]
<i>Sphingomonas faeni</i>	Finger millet	Cold stress	Srinivasan <i>et al.</i> [215]
<i>Azospirillum brasilense</i>	Wheat	Cold stress	Turan <i>et al.</i> [146]
<i>B. megaterium</i>	Wheat	Cold stress	Turan <i>et al.</i> [146]
<i>Bacillus subtilis</i>	Wheat	Cold stress	Turan <i>et al.</i> [146]
<i>Raoultella terrigena</i>	Wheat	Cold stress	Turan <i>et al.</i> [146]
<i>Serratia nematodiphila</i> PEJ1011	Pepper	Cold stress	Kang <i>et al.</i> [216]
<i>A. brasilense</i>	Wheat	Drought	Creus <i>et al.</i> [217]
<i>Pseudomonas fluorescens</i>	Foxtail millet	Drought	Niu <i>et al.</i> [218]
<i>P. putida</i>	Sunflower	Drought	Sandhya <i>et al.</i> [219]
<i>Raoultella planticola</i> YL2	Maize	Drought	Gou <i>et al.</i> [220]
<i>Pseudomonas libanensis</i>	Brassica	Drought	Ma <i>et al.</i> [149]
<i>Pseudomonas reactans</i>	Brassica	Drought	Ma <i>et al.</i> [149]
<i>Aneurinibacillus aneurinilyticus</i>	Chilli	Drought	Patel <i>et al.</i> [150]
<i>Acinetobacter calcoaceticus</i>	Foxtail millet	Drought	Kour <i>et al.</i> [52]
<i>Klebsiella variicola</i>	Soybean	Flooding	Kim <i>et al.</i> [221]
<i>Pseudomonas aeruginosa</i>	Wheat	Heavy metal	Islam <i>et al.</i> [222]
<i>Bacillus safensis</i>	Wheat	High temperature	Sarkar <i>et al.</i> [223]
<i>P. putida</i>	Wheat	High temperature	Ali <i>et al.</i> [144]
<i>Burkholderia seminalis</i>	Rice	Low pH	Panhwar <i>et al.</i> [147]
<i>Burkholderia thailandensis</i>	Rice	Low pH	Panhwar <i>et al.</i> [147]
<i>Sphingomonas pituitosa</i>	Rice	Low pH	Panhwar <i>et al.</i> [147]
<i>Achromobacter piechaudii</i>	Tomato	Salinity	Mayak <i>et al.</i> [224]
<i>Arthrobacter protophormiae</i>	Wheat	Salinity	Barnawal <i>et al.</i> [225]
<i>A. brasilense</i>	White clover	Salinity	Khalid <i>et al.</i> [226]
<i>Bacillus aquimaris</i> DY-3	Maize	Salinity	Li and Jiang [227]
<i>Bacillus atrophaeus</i> EY6	Strawberry	Salinity	Karlidag <i>et al.</i> [228]
<i>Bacillus mojavensis</i>	Wheat	Salinity	Pourbabaee <i>et al.</i> [229]
<i>Bacillus pumilus</i>	Rice	Salinity	Jha and Subramanian [230]
<i>Bacillus spharicus</i>	Strawberry	Salinity	Karlidag <i>et al.</i> [228]
<i>Bradyrhizobium japonicum</i>	Soyabean	Salinity	Méthé <i>et al.</i> [231]
<i>Kocuria erythromyxa</i>	Radish	Salinity	Yildirim <i>et al.</i> [232]
<i>Planococcus rifietoensis</i>	Wheat	Salinity	Rajput <i>et al.</i> [233]
<i>Pseudomonas pseudoalcaligenes</i>	Rice	Salinity	Jha and Subramanian [230]
<i>Pseudomonas syringae</i>	Maize	Salinity	Nadeem <i>et al.</i> [234]
<i>Staphylococcus kloosii</i>	Radish	Salinity	Yildirim <i>et al.</i> [232]
<i>Staphylococcus kloosii</i> EY37	Strawberry	Salinity	Karlidag <i>et al.</i> [228]
<i>Stenotrophomonas maltophilia</i>	Wheat	Salinity	Singh and Jha [235]
<i>Brevibacterium casei</i>	Groundnut	Salinity	Shukla <i>et al.</i> [145]
<i>Brachybacterium saurashtrense</i>	Groundnut	Salinity	Shukla <i>et al.</i> [145]
<i>Bacillus subtilis</i>	Barley	Salinity	Patel <i>et al.</i> [148]
<i>B. megaterium</i>	Barley	Salinity	Patel <i>et al.</i> [148]
<i>Bacillus pumilus</i>	Rice	Salinity	Kumar <i>et al.</i> [236]

*A. brasilense*: *Azospirillum brasilense*, *B. megaterium*: *Bacillus megaterium*, *P. putida*: *Pseudomonas putida*

## 5. CONCLUSIONS

Microbial diversity is fundamental for the conservation and maintenance of global genetic resources. The phyllosphere, endophytic, and rhizosphere are a hot spot for bacterial diversity that mainly expressed as functions adaptation that assist in plant growth promotion. Beneficial PGP soil and phyto-microbiomes represent a variety of soil microbial strain that can improve the growth of their plant host, when the host and PGP microbiomes are grown in association. Such types of microbes benefit by metabolites utilization as a nutrient for their development and growth that are secreted by roots of plant and stimulate the growth through variety of mechanisms such as growth stimulating hormones production and plant pathogens suppression. In the plant rhizosphere, beneficial interactions between plant-microbe are known to be important determinants of plant and soil health. The agri-food sector and agriculture is expected to grow toward sustainable development, while increasing its productivity and simultaneously protecting the natural resource. The global interest has been shifted toward beneficial microbes of rhizosphere and bulk soil in natural agro ecosystems contributing to productivity of plant and soil health can be exploited as bioinoculants (biofertilizers and bioagents) to increase more crop production.

## 6. AUTHORS' CONTRIBUTIONS

All authors made substantial contributions to conception and design, acquisition of data, or analysis and interpretation of data; took part in drafting the article or revising it critically for important intellectual content; agreed to submit to the current journal; gave final approval of the version to be published; and agreed to be accountable for all aspects of the work. All the authors are eligible to be an author as per the International Committee of Medical Journal Editors (ICMJE) requirements/guidelines.

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## 8. CONFLICTS OF INTEREST

The authors report no financial or any other conflicts of interest in this work.

## 9. ETHICAL APPROVALS

This study does not involve experiments on animals or human subjects.

## 10. DATA AVAILABILITY

Not Applicable.

## 11. PUBLISHER'S NOTE

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