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1. Soil Microbes and Their Role in Plant Growth Promotion

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Abstract:

Soil microbes, encompassing bacteria, archaea, and fungi, play pivotal roles in facilitating plant growth and development through a myriad of interactions and processes. Bacteria, such as nitrogen-fixing rhizobia and phosphate-solubilizing bacteria, contribute to nutrient availability by converting atmospheric nitrogen into forms usable by plants and solubilizing phosphorus from organic or mineral sources, respectively. Archaea, though less studied in this context, are increasingly recognized for their potential roles in nutrient cycling and soil fertility. Additionally, fungi, including mycorrhizae and endophytes, form symbiotic relationships with plant roots, enhancing nutrient uptake and promoting plant resilience to stressors. These microbes aid in nutrient cycling, disease suppression, and the production of growth-promoting compounds like phytohormones and antibiotics. Moreover, they participate in the degradation of organic matter, influencing soil structure and enhancing water retention capacity. Understanding the intricate interactions among soil microbes and their impact on plant growth is crucial for sustainable agriculture practices aimed at maximizing crop productivity while minimizing environmental impacts, ultimately contributing to global food security.

Keywords:

Bacteria, Soil Microbes, Plant Growth, Microbial Diversity, Plant-Soil System.

1.1 Introduction:

The earth's surface is naturally covered in soils, which are the interface of three different material states: liquids, solids (such as geological and decomposing organic elements), and (air in soil pores) and gases (water). Every soil is a distinct result of the interplay between its geological parent material, its history of glaciation and geomorphology, its biota's existence and activity, its land use and disturbance history, and other factors. All terrestrial ecosystems are built on the foundation of soils, which support various plants, algae, bacteria, archaea, fungi, insects, annelids, and other invertebrates. The food or nutrients these soil dwellers supply supports the species living above and below ground [1].

Furthermore, soils are essential for protecting and stabilising freshwater habitats. As such, soils play a critical role in human communities. Soils influence the majority of ecosystem services that humans rely on, including the foundation upon which we and our structures are built and the generation of food, construction materials, and other resources [2].

Numerous and frequently crucial roles are played by bacteria, fungi, archaea, and soil microorganisms in various ecological services. Because of the enormous metabolic diversity of soil microorganisms, all main elements (such as C, N, and P) are either driven by or influenced by their activities. This cycling has an impact on the composition and operations of soil ecosystems as well as the soils' capacity to offer benefits to humans.

What are Bacteria, Archaea and Fungi?

On Earth, bacteria and archaea are the tiniest self-sufficient single-celled creatures. The typical diameter of a cell is between 0.5 and 1.0 µm. Cocci can include both bacteria and archaea. Some bacteria frequently found in soils, like the Actinomycetales, can create branching filaments and rods or spirals. As most do not have a genuine nucleus that is membrane-bound, their DNA is free to roam around throughout the cytoplasm of the cell. A single circular molecule of double-stranded DNA makes up their genome in most cases, yet cells may potentially include smaller DNA elements called plasmids. Like all other creatures, bacteria and archaea depend on carbon to supply the building components for their cell walls. To power the reactions involved in cell formation and metabolism, they also need energy. Some bacteria need oxygen to grow, while most archaea and other bacteria employ alternate electron acceptors, such as nitrate and sulphate (i.e., they respire nitrate and sulphate). Oxygen may be hazardous to these anaerobic species. Microbes are often divided into two categories: autotrophs and heterotrophs [1]. While heterotrophs employ organic carbon compounds as a source of carbon and energy, autotrophs use energy from sunlight or inorganic compounds (such as Fe^{2+}, nitrate, or nitrite) to fix atmospheric carbon dioxide to make carbs, lipids, and proteins.

Although archaea were once assumed to only be found in severe conditions and were frequently referred to as "extremophiles," we know that they are widely distributed and may be found in many different environments, including soil, alongside bacteria. It is challenging to differentiate between bacteria and archaea based just on morphology. All life, however, can be separated into three domains using molecular phylogenetic techniques based on a comparison of 16S ribosomal rRNA sequences; Archaea is more closely linked to Eukarya (all multicellular organisms) than Bacteria [3]

Compared to bacteria or archaea, fungi are more closely related to plants and animals since they belong to the eukarya class of life. The chromosomes of fungal cells include DNA, and like the nuclei of all eukarya, including humans, these are membrane-bound. Additionally, they have organelles like mitochondria that are membrane bound. Glucans and chitin make up the cell wall of fungi. As heterotrophic creatures, fungi eat decaying stuff by default, using this as their primary food source. While some fungi occur as single-celled organisms, generally referred to as yeasts, many grow as hyphae, which are cylindrical thread-like structures, 2–10 µm in diameter. The hyphae may be septate – divided into compartments separated by cross walls – or non septate. Fungi reproduce by both sexual and asexual means. Both processes produce spores: a general term for resistant resting structures. Like bacteria and archaea, fungi are extremely diverse and their unique life-history strategies allow them to serve a wide variety of ecological roles, for example decomposers, mutualists, endophytes of plants, pathogens, and even predators. Fungal hyphae are foundational components of soil food webs because they are forage for grazing soil biota [3-4].

Table 1.1: Role of soil microbes in provisioning and regulating services provided by soil ecosystems (Dominati *et al*., 2010)

Soil service	Descriptor	Role of soil microbes
Provisioning services – products obtained from ecosystems		
Physical support	Soils form the surface of the earth and represent the physical base on which animals, humans and infrastructures stand. Soils also support animal species that benefit humans (e.g. livestock).	Microbes contribute to soil formation through nutrient cycling and organic matter production. Microbial products are critical to soil aggregation, improved soil structure making soil more habitable for plants.
Raw materials	Soils can be a source of raw materials (e.g. peat for fuel and clay for potting).	Soil microbes produce antimicrobial agents and enzymes used for biotechnological purposes.
Growth medium for plants	Humans use plants for food, building, energy, fibre, medicines and more. By enabling plants to grow, soils provide a service to humans. Soils physically support plants and supply them with nutrients and water.	Soil microbes mobilise nutrients from insoluble minerals to support plant growth.
Regulating services – enable humans to live in a stable, healthy and resilient environment		
Buffering water flows	Soils can store and retain quantities of water and therefore can mitigate and lessen the impacts of extreme climatic events (e.g. limit flooding). Soil macroporosity and hydrological processes like infiltration and drainage impact on this service.	Soil macropores are formed by plant roots, earthworms and other soil biota, which may depend on soil microbes as food or for nutrients.
Nutrient cycling	Soil is the site of the decomposition of organic materials and the mobilisation of nutrients in bedrock and soil aggregates. Soil is also the site of the oxidation and reduction of nutrient elements, symbiotic N-fixation and photoautotrophic activity.	The activities of soil bacteria, archaea and fungi drive nutrient cycling in soils and are involved in weathering minerals.
Recycling of wastes and detoxification	Soils absorb, detoxify, and recycle applied wastes (e.g. ef- fluent disposal), agrochemicals, and spills of fuels and oils, reducing potential	Microbial processes like mineralisation and immobilisation are responsible for this service. Detoxifying

Soil service	Descriptor	Role of soil microbes
	harm to humans and to organisms useful to humans.	microbes may be limited by the availability of soil nutrients (e.g. N or P), which in turn depends on soil microbial activities.
Filtering of contaminants	If pollutants (e.g. excess nutrients, exotic microbes, metals, organic compounds) are leached from soils, they can con- taminate aquatic ecosystems and threaten human health. Soils absorb and retain solutes and pollutants, avoiding their release into water.	In concert with the clay and organic matter content of soils, microbial products contribute to both the hydrophobicity and wettability of soils, impacting on the ability of soils to filter contaminants.
Habitat for biodiversity	A very large component of global biodiversity occurs in soils. Some organisms have above-ground life stages or are food resources for above-ground species. Soils are a reservoir for resting phases of organisms (e.g. seeds, fungal spores) and thus are critical for the rejuvenation of communities.	Soil bacteria, archaea, and fungi comprise the vast majority of the biological diversity on earth. Further, they are the founda- tion of soil food webs thereby underpinning the diversity of higher trophic levels. Interactions among soil microbes and plants often determine plant biodiversity.
Biological control of pests, weeds and patho- gens	Soils provide habitat to beneficial species that regulate the composition of communities and thus prevent proliferation of herbivores and pathogens. This service depends on soil properties and the biological processes driving inter- and intra-specific interactions (symbiosis, competition, host–prey associations).	Beneficial species include bacteria, archaea, and fungi that support plant growth through increasing nutrient availability and by outcompeting invading pathogens.
Carbon storage and regulation of greenhouse gas emissions	Soils play an important role in regulating many atmospheric constituents, impacting on air quality, and on regional and global climate. Soils store carbon as stable organic matter off-setting CO_2 emissions and are home to microbes that release nitrous oxide (N_2O) and methane (CH_4).	By mineralising soil carbon and nutrients, microbes are major determinants of the carbon storage capacity of soils. Denitrifying bacteria and fungi and methane producing and consuming bacteria regulate nitrous oxide (N_2O) and methane (CH_4) emissions from soils.

1.2 Microbial Diversity and its Interaction with Plant-Soil System:

The bodies among the vast resources of activities of microscopic diversity include soil microorganisms, such as bacteria, algae, fungus, actinomycetes, protozoa, and infectious agents as viruses [5]. These soil microorganisms have both beneficial and detrimental effects in addition to their many useful roles. The effects of soil biota are complex and varied in the soil profile since the same action might have different effects depending on where it is located [6]. However, plants engage in a wider range of interactions with these soil-dwelling microbes, expanding the range of biological possibilities (competitive, exploitative, neutral, commensal, and mutualistic). But given the current state of affairs, more research is being done on the harmful impacts that are alleviating, like infection and herbivory [7]

The impact of ecological stress aspects must be taken into consideration, as they affect proper management of the interactions between crop-microbiome since the interactions between plant and microscopic communities are primarily influenced by biological factors and various agronomic managements in the current global revolution [8]. Given the intricate relationships between microbes and the plant-soil system, it is not surprising that the establishment of high-fertility soil has resulted from hundreds of years of soil "evolution." [9].

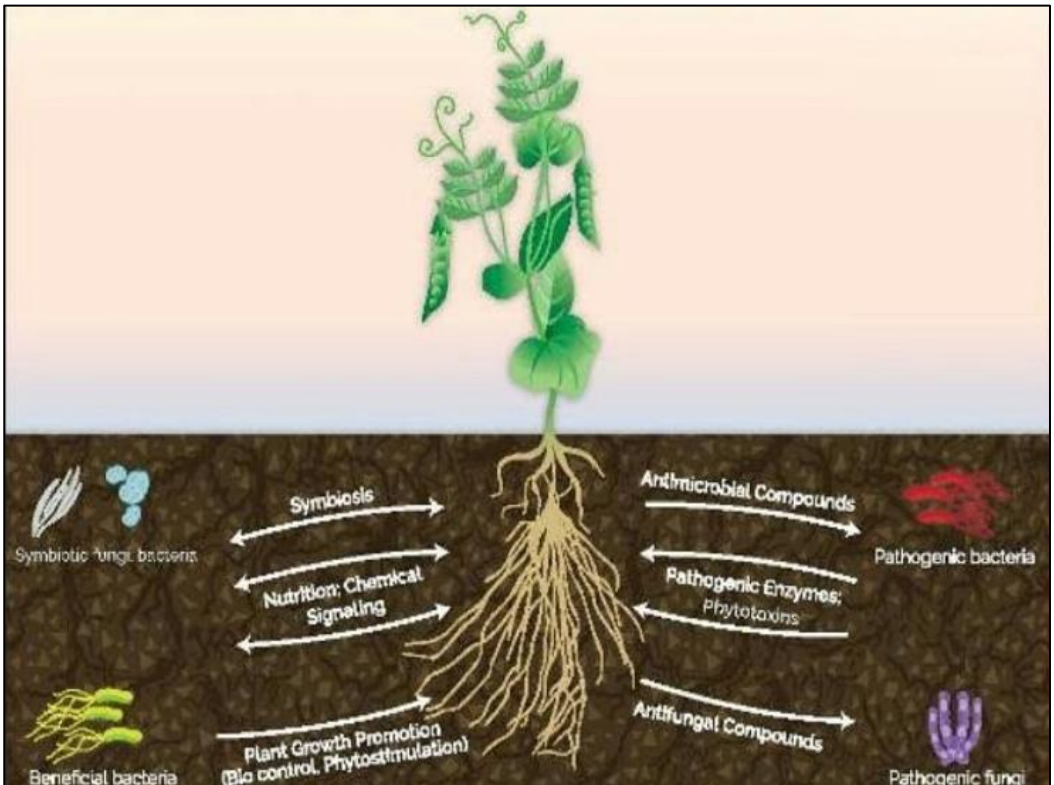

Figure 1.1: Interactions between microbial communities and plant (Source: Google).

Beneficial Aspects of Microbes:

The soil fertility and its formation from mineral bedrock involves a multifarious interaction of chemical, physical and biological processes. The development rate of the soil is controlled by some factors such as topography, climate, time, bedrock type, plants and microbes [10] that's why the status of nutrients is determined by the quality and identification of microbes in soil [11]

1.3 Plant-Growth-Promoting Rhizobacterias (PGPRs):

One of the important categories of soil microbes is PGPRs.In the natural environment, PGPRs are soil dwellers that aggressively reach plant roots to increase plant strength. In crop cultivation, its use can improve long-term food production, support the environment, and support the modest use of agrochemicals. Better seedling growth, early nodulation and function, as well as enhanced leaf surface area, vigour, biomass, phytohormone, nutrient, water, and air uptake, and enhanced carbohydrate accumulation and production in many plant species are all attributed to PGPR. Currently, many products on the market are composed of one or combinations of plant-growth-promoting rhizobacteria (PGPRs). Soil microbes that have been classified as PGPRs include Azospirillum, Bacillus, Pseudomonas, Agrobacterium, Azotobacter, Alcaligenes, Clostridium, Beijerinckia, Rhizobium, Arthrobacter, Serratia, Enterobacter, Phyllobacterium, Burkholderia, Klebsiella, Vario-vovax, and Xanthomonas. These genera have been shown to have a positive impact on plant growth.

Table 1.2: Microorganisms with different beneficial effects in different crops

Bacterial Strains	Crop	Evaluation Conditions	Highlights	Reference
Enterobacter hormaechei, *Rhizobium spp.*, *Pseudomonas fluorescence*, and AAULE51 (undetermined)	Pepper	Greenhouse using inoculated seeds	Plants produced from inoculated seeds exhibited higher shoot and root lengths in addition to showing resistance to drought stress.	Admassie *et al*., 2022 [12]
Bacillus subtilis (MW644678, MW644686, MW644650, MW644649, MH845220, MZ488941, MZ488846), *Bacillus amyloliquefaciens* MW644651, *Bacillus safensis* MK212368,	Sugar beet	Under greenhouse conditions, using sugar beet seeds treated with each bacterium.	Antifungal activity against Sclerotium rolfsii Sacc and a reduction in the severity and incidence of root rot disease. Furthermore, increases in length of shoots and roots and plant fresh and dry weight were recorded.	Farhaoui *et al*., 2022 [13]

Bacterial Strains	Crop	Evaluation Conditions	Highlights	Reference
and *Bacillus halotolerans* MW644679				
Streptomyces corchorusii TKR8, *Streptomyces corchorusii* JAS2 and *Streptomyces misionensis* TBS5	Rice	Greenhouse conditions using inoculated seeds	Streptomyces-treated plants exhibited improvement in rice plants' growth and grain yield. Additionally, a reduction in the disease severity of bacterial panicle blight (BPB) was observed in treated plants.	Ngalimat *et al*., 2022 [14]
Plant Growth-Promoting Bacteria (PGPB) consortia	Oilseed rape	Pot experiment using Cd naturally polluted soil.	PGPB-based consortia promoted plant growth, increased Cd uptake of oilseed rape, Cd phytoextraction, and Cd removal from soil. Further, consortia increased microbial carbon, urease and sucrase activities, and the relative abundance of selected bacteria g	Wang *et al*., 2022 [15]
Enterobacter cloacae and *Burkholderia cepacia*	Garlic	In vitro growth	Both growth and physiological attributes of garlic were increased when their meristems were inoculated with the PGPB.	Costa Júnior *et al*., 2020 [16]
Methylobacterium oryzae MNL7 and *Paenibacillus polymyxa* MaAL70	Flooded paddy	100 g of field soil deposited into cork sealed beakers and f illed up to 1.5 cm of water	Grain yield and grain nutrient quality were improved by the co-inoculation; meanwhile, methane emission was reduced in comparison with uninoculated treatments.	Rani *et al*., 2021 [17]

Bacterial Strains	Crop	Evaluation Conditions	Highlights	Reference
Paenibacillus taichungensis, Enterobacter sp., Rhizobium sp., Paenibacillus sp., Pseudomonas sp., and *Paenibacillus pabuli*	Walker's cattleya orchid	In vitro inoculation of seedlings obtained by micropropagation of Cattleya walkeriana.	Potential effect on improved nutrient acquisition and overall growth. Antioxidant enzyme activity and non-enzymatic antioxidants were increased.	Andrade *et al*., 2023 [18]
Pseudomanas gessardi EU LWNA-25 and *Erwinia rhapontici* EU-B1SP1	Amaranth	Controlled (pot) and natural (experimental farm) conditions.	Bacteria used as microbial consortia enhanced the growth of Amaranthus crops, expressed as the growth, grain, and yield.	Devi *et al*., 2022 [19]
Acinetobacter calcoaceticus P23, *Pseudomonas fulva* Ps6 and *Chryseobacterium* strains	Duckweed	Biomass production using a low nitrogen content and high salt food factory effluent (WW).	PGPRs promoted the growth of the crop under standard conditions but not when WWwasused.	Khairina *et al*., 2020 [20]
Azotobacter chroococum and *A. vinelandii*	Eggplant	Root inoculation in plants exposed to different levels of drought stress.	Inoculated plants under drought stress exhibited higher dry matter production, leaf relative water, ions (K, Ca, and Mg), protein in roots, phenolic compounds, and proline.	Kiran *et al*., 2022 [21]

1.4 Direct and Indirect Mechanisms of Microorganisms in Plants:

PGPRs can directly or indirectly increase their hosts' fitness. The direct methods that encourage plant development are among them. These include the synthesis of hormones such as gibberellins, cytokinins, and auxins. in addition to phosphorus solubilization and nitrogen fixation. One or more plant-pathogenic organisms' ability to operate is inhibited by the indirect processes [21]. These main mechanisms are the production of antibiotics, enzymes that degrade the cell wall and antioxidants, the inhibition of the pathogen quorum, induced systemic resistance, and iron sequestration by bacterial siderophores.

The reduction in ethylene levels by the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase is also classified as a direct mechanism of promotion (Figure 1.2) [22-24].

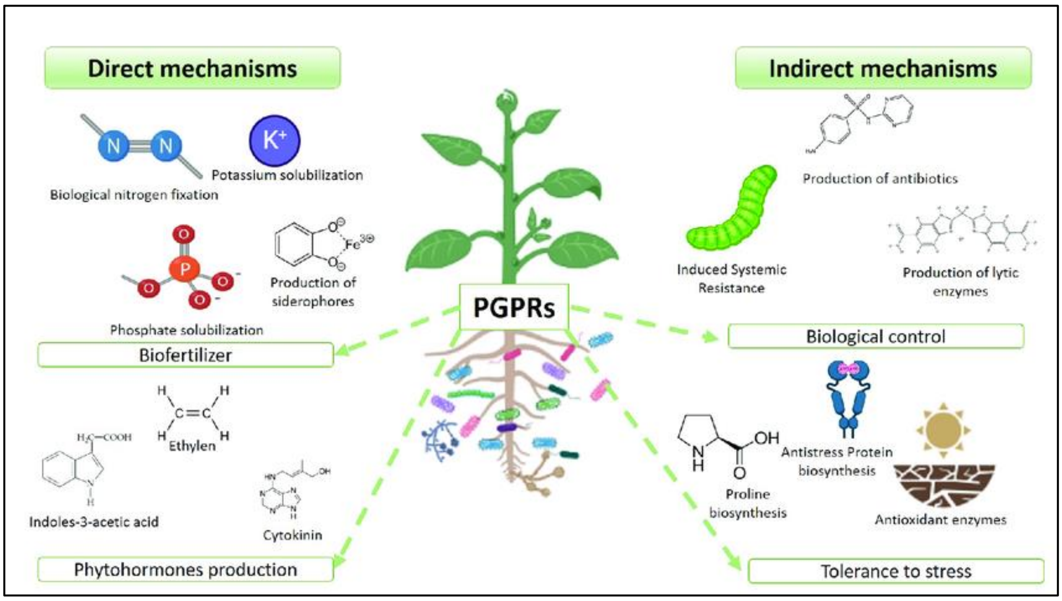

Figure 1.2: Direct and indirect mechanisms of PGPRs

It has been observed that 80% of bacteria colonising the rhizosphere are capable of producing auxin, one of the most commonly reported metabolites for the encouragement of plant growth. When plants are inoculated with PGPRs, reports of root length reduction, for decades, and a rise in the quantity of root hairs and lateral roots have been made. Auxin production by bacteria has been linked to these morphological changes in the roots, and investigations with plant mutants with altered IAA production have validated this involvement [25]. The plant-growth-promoting effect of bacteria in which auxin is involved is known as phytostimulation. Root nodules have been reported to contain more auxin than non-nodulated roots [26]. On the other hand, tetracyclic diterpenoid carboxylic acids with C20 or C19 carbon skeletons are included in the broad class of gibberellins [27]. In addition to increasing the rate of photosynthesis and the concentration of chlorophyll, gibberellins are known to stimulate growth and activate growth processes, including stem elongation, seed germination, flowering, and fruit setting [28, 29,30]. *Bacillus* species, *Achromobacter xylosoxidans*, *Gluconobacter diazotrophicus*, *Acinetobacter calcoaceticus*, *Rhizobium*, *Azotobacter* species, *Herbaspirillum seropedicae*, *Enderococcus faecium*, *Pseudomonas* species, *Promicromonospora* species, and *Azospirillum* species are among the PGPR genera that can manufacture gibberellins [31, 32].Cytokinins are another type of phytohormone generated by bacteria. In metastatic tissues, they regulate cell differentiation and revert apical dominance, root elongation, seed germination, flower and fruit development, and interactions between plants and pathogens [33,34]. Methylobacterium, *Sinorhizobium meliloti*, and Bacillus subtilis are the common parasitic gramme positive bacteria [35, 36]. Nitrogen is one of the most important macronutrients for plant growth. The abundance of nitrogen in the atmosphere is approximately 78%, and plants cannot assimilate it. Rhizobia are diazotrophs (prokaryotic organisms that carry out dinitrogen fixation) that form a symbiotic association with legumes. The word Rhizobium comes from the Greek words: "rhiza" which refers to root, and "bios" which refers to life. *Rhizobium* species like *R. leguminosarum* can be found in soil.

However, the root of leguminous plants (lentil, sweetpea etc) is their primary habitat. In the soil, various leguminous plants release various exudates (dicarboxylic acids etc) that attract *Rhizobium* species. Rhizobia are free living in the soil until they can sense flavonoids, derivatives of 2-phenyl-1.4-benzopyrone, which are secreted by the roots of their host plant. Flavonoids play an important role attracting the bacteria given that they are easily absorbed through the membrane of the organisms (passively). Once the bacteria detect these chemicals, it triggers the accumulation of a large population of cells and eventually attachment to root hairs. *Azotobacter* is Gram-negative, motile, pleomorphic aerobic bacterium which produces thick-walled cysts and may produce large quantities of capsular slime. *Azotobacter* is a non- nodule forming asymbiotic diazotrophs which plays an important role in N cycle in nature- binding atmospheric nitrogen which is inaccessible to plants and releasing ammonium ions to soil. Members of these genera are mesophilic, which require optimum temperature of about 30ºC and are mostly found in neutral and alkaline conditions. The first representative of the genus, *Azotobacter chroococcum*, was discovered and described in 1901 by the Dutch microbiologist and botanist Martinus Beijerinck. It respires aerobically & uses the OM present in the soil to fix atmospheric nitrogen asymbiotically and receiving energy from redox reactions using organic compounds as electron donors. *Azospirillum* is a Gram-negative, microaerophilic, non-fermentative and nitrogen-fixing bacterial genus from the family of Azospirillaceae. It is a primary inhabitant of soil, the rhizosphere, and intercellular space of root cortex of gramineous plants. It is found in association with root system as associative symbiosis. It is applied to non-legumes like maize, barley, oats, sorghum, millet, Sugarcane, rice etc. The inoculation of nitrogen-fixing microorganisms in seeds, seedlings, roots, or soil stimulates plant growth, improves soil quality, and maintains the nitrogen level in the soil [37].

A group of heterotrophic microorganisms solubilize this fixed phosphorous by producing organic acids and enzymes and make them available to the crops. This group of microorganisms is called Phosphorous Solubilizing Microorganisms. Microorganisms involved in phosphorus acquisition include mycorrhizal fungi and PSMs. Among the soil bacterial communities, ectorhizospheric strains from *Pseudomonas* and *Bacilli*, and endosymbiotic rhizobia have been described as effective phosphate solubilizers. Strains from bacterial genera *Pseudomonas*, *Bacillus*, *Rhizobium* and *Enterobacter* along with *Penicillium and Aspergillus* fungi are the most powerful P solubilizers. *Bacillus megaterium, B. circulans, B. subtilis, B. polymyxa, B. sircalmous, Pseudomonas striata,* and *Enterobacter* could be referred as the most important strains. A nemato fungus *Arthrobotrys oligospora* also can solubilize the phosphate rocks. Another crucial nutrient required by plants is iron (Fe). However, similar to the previous nutrients, it is also unavailable to plants since it is insoluble in Fe3+, associated with hydroxides and oxyhydroxides [38]. Some PGPRs can secrete siderophores in soil: phenolates, catecholates, hydroxamates, carboxylates, or mixed types. Siderophores are small peptide molecules that bind Fe^{3+} and make it available to cells [39]. Some siderophores also show an affinity for Pb, Cd, Zn, Cu, Co, Mo, and even for As. PGPRs with this ability are *Pseudomonas, Bacillus, Rhizobium, Azotobacter, Enterobacter,* and *Serratia* [40].

K is the third most important plant macronutrient after nitrogen and phosphorus. It is absorbed from soil primarily in the form of K+ and is required in the plants for early growth, production, and modification of proteins, maintenance of water use efficiency, stand persistence, longevity, etc.

There is a mutual relationship between soil microflora (bacteria, fungi, algae, protozoa, nematode etc.). Solubilization of minerals present in soil environment, and these interactions have been extensively studied by many investigators to improve the nutrient (K) status of soil for optimum crop growth. Microflora adopt several mechanisms to solubilize complex soil minerals thereby enhancing plant growth and development for higher crop production.

Table 1.3: Microorganisms involves in potassium solubilization (Meena *et al*., 2016)

Microorganisms: Bacteria and Fungi	**Organic acid Produced**
1.*Aspergillus niger*	1.Succinic
2.*Pencillium regulosum*	2.Citric, Gluconic
3.*Aspergillus flavus*	3.Citric, Oxalic, Gluconic, Succinic
4.*Aspergilluscandidus,Aspergillusflavus*	4.Malic, Gluconic, Oxalic
5.*Serratia marcescens (CC-BC14)*	5.Citric, Lactic
6.*Chryseobacterium (CC-BC05)*	6.Citric
7.*Trichoderma sp,A.terreus,A.wenti, Pencillium sp,Fusarium oxysporium*	7.Lactic, Malic, Acetic, Tartaric, Fumaric, Citric, Gluconic
8.*Aspergillus niger,Pencillium sp,*	8.Oxalic,Citric
9.*Pseudomonas Trivalis (BIHB 769)*	9.Gluconic, Lactic, Succinic, Formic, Malic
10.*Aspergillus awamori S19*	10.Malic, Citric, Fumaric, ,Oxalic
11.*Enterobacter sp.FS-11*	11.Malic, Gluconic
12.*Aspergillus niger FSI, Pencillium islandicum FS30*	12.Citric, Gluconic, Oxalic

The synthesis of antibiotics, including aerugin, azomycin, cepafungins, kanosamine, karalicin, phenazine-1-carboxylic acid (PCA), pyrrolidinine, butyrolactones, surfactin, fengycin, and rhamnolipids, is the most significant of the indirect methods [49].

They have antiviral, anthelmintic, antifungal, and antibacterial properties. Phytopathogenic fungi like Rhizoctonia, Fusarium, Pythium, Alternaria, Phytophthora, and Botrytis can be inhibited by bacterial peptides. PGPRs from the genera Streptomyces, Pseudomonas, and Bacillus have been used to treat plant diseases in a variety of commercially significant crops [41,42, 43].

Certain organisms can create enzymes that can break down the fungal cell wall of certain phytopathogens. Protease, lipase, chitinase, and 1,3-glucanase are some of the enzymes that have this capacity; they break down the components of fungal cell walls [44–46]. Conversely, plants generate reactive oxygen species (ROS) in response to various forms of stress, which are linked to oxidative cell damage.

Consequently, certain microorganisms can generate an antioxidant defence system for plants. One example of these mechanisms is the generation of antioxidant enzymes, which include catalase (CAT), superoxide dismutase (SOD), and peroxide dismutase (POD). These enzymes are produced by certain PGPR genera, including *Bacillus licheniformis, Bacillus amyloliquefaciens,* and *Pseudomonas fluorescens* [47–49]. N acyl homoserine lactones (AHL) are signalling molecules that bacteria can use to communicate. They can also be used to detect changes in the environment and the density of the bacterial population. Because they can interact through molecules, some plant-pathogenic bacteria can develop more virulence [50]. One way to prevent infections from communicating with one another is to disrupt quorum sensing using PGPRs, which can release certain enzymes like lactonase. This will reduce the pathogens' pathogenicity and stop them from growing in the plant [51]. *Bacillus, Agrobacterium, Rhodococcus, Streptomyces, Arthrobacter, Pseudomonas, and Klebsiella* are some of the taxa that possess this ability [52].

Plants can defend themselves by developing induced systemic resistance (ISR), which is brought on by pathogen invasion, wounds, or root colonisation. PGPRs can induce induced systemic resistance (ISR) through their metabolites or cell wall components [53]. Certain phytopathogen-induced stress regulators (PGPRs) like *Bacillus subtilis and Pseudomonas* sp., when exposed to phytopathogens (e.g., *Rhizoctonia, Fusarium, Pythium, Alternaria, Ralstonia, Phytophthora, and Botrytis*), generate antimicrobial peptides and induce ISR [54,55].

Releasing root exudates allows plants to choose their microbiota. Chemotaxis is the process by which low molecular weight molecules (such as sugars, amino acids, and organic acids) and high molecular weight compounds (such as polysaccharides, mucilage proteins, and vitamins) draw microbes to the rhizosphere [56]. Bacillus subtilis FB17 recognises its host, but not other Bacillus species, thanks to the presence of L-malic acid and other nutrients [57]. Algae, archaea, arthropods, bacteria, fungus, nematodes, protozoa, and viruses are examples of the microbiota that can be found in the rhizosphere of plants [56]. In order to flourish and endure in the rhizosphere, microorganisms have evolved coping mechanisms. They can prevent the harmful effects of antimicrobial metabolites released by plants (such as phytoalexins, flavonoids, and alkaloids) by breaking them down. The following review addresses these relationships' molecular processes from a transcriptomic perspective.

While the rhizosphere has historically been the primary source of microbes that promote growth, the Additionally, the phyllosphere is home to a variety of microbes with exceptional metabolic capability. The term "phyllosphere" describes the plant's aerial components, such as the stems, leaves, fruits, and reproductive organs [58]. The majority of the phyllosphere is made up of leaves, each of which contains 106–108 bacterial cells/cm^2 [59]. In addition to coming from endophytes, phytosphere microbiota can also originate from the air, precipitation, irrigation, vectors, and soil dust. But not all bacteria can withstand exposure to UV light, famine for nutrients, and changes in the humidity and temperature of their surroundings [60]. Additionally, they need to be able to adhere to the cuticle of leaves, which is a helpful quality for using bacteria as foliar-applied bioinoculants. They then release volatile chemical compounds called siderophores. Additionally, bacteria in the phyllosphere can cause plants to mount a defence mechanism against phytopathogen invasion by increasing the synthesis and accumulation of phytoalexins, alkaloids, and glucanases [60].

Additional responsibilities of These microorganisms are involved in the regulation of flowering, the growth of seeds and fruits, defence against pollutants and pesticides, enhancement of crop yields, and cycling of carbon and nitrogen [62].

As phyllosphere inhabitants, *Sphingomonas, Streptomyces, Pseudomonas, Methylobacterium,* and *Bacillus* are frequently observed in maize, rice, soybean, sugarcane, and fruit trees [61].

Some of them use stomata, lenticels, and hydathodes to colonise plants, and they spread to other tissues by way of the xylem and phloem systems [63]. Combining rhizosphere and phyllosphere bacteria would be a novel way to create biofertilizers that address important plant nutrition requirements.

1.5 Characteristics of an ideal PGPR:

If a rhizobacterial strain contains certain plant growth-promoting properties and may boost plant development after inoculation, it is termed as putative PGPR [27]. The following are the characteristics of an optimal PGPR strain:

It should be biosphere-friendly and rhizosphere-competent.

- Upon inoculation, it should colonize the plant roots in substantial quantities.
- It should be able to aid in the development of plants.
- It should be capable of a wide range of actions.
- It has to get along with the other microorganisms in the rhizosphere.
- It must be resistant to physicochemical variables such as heat, dehydration, radiation, and oxidants.
- It should outperform current rhizobacterial communities in terms of competitive abilities.

1.5.1 Types of PGPR:

Plant growth-promoting microbes are strongly associated with root cells of the plants and are classified as follows:

– Intracellular PGPR (iPGPR/symbiotics)

– Extracellular PGPR (ePGPR/free living)

A. Extracellular rhizobacteria that stimulate plant development:

It grows in the spaces between root cortex cells or on the rhizosphere. The genera that make up the ePGPR are: *Burkholderia, Erwinia, Flavobacterium, Arthrobacter, Pseudomonas, Micrococcus, Azotobacter, Bacillus, Azospirillum, Caulobacter, Chromobacterium,* and *Agrobacterium* [64].

B. Rhizobacteria that promote the growth of intracellular plants:

It is mostly located inside the root cells, where a special nodular structure holds a population of bacteria that can fix atmospheric nitrogen, especially advantageous to terrestrial plants [65]. *Bradyrhizobium, Rhizobium, Mesorhizobium, Allorhizobium*, and Frankia are the genera that are included in iPGPR. The iPGPR is present inside root cells, typically in structures known as nodules that are specialised growths. The plant tissue's intercellular ePGPR is found in the intercellular gaps of the root cortex or surrounding the root surface (rhizoplane) [66].

Microbial secondary metabolites for plant growth and its mechanism of action:

Beneficial microorganisms are known to create a variety of naturally occurring chemicals that are heterogeneous and are essential for performing various fundamental tasks such as metal transport to plants, competition against dangerous diseases, and symbiosis with nearby microbes [67]. These substances, which are produced by beneficial soil bacteria in the late of their cell cycle event, are detrimental to the development and growth of plants, but can improve resistance, signalling with neighbouring beneficial microorganisms, and plant adaptation to unfavourable conditions [68]. The fact that these metabolites are used in a variety of industries, including the food, chemical, and medical sectors, makes these microbial SMs essential for human health as well [69,70]. Of all the metabolites, amino acids, ethanol, and lactic acid are the principal microbial metabolites that are necessary for the growth, development, and reproduction of organisms and producers. But for other living things' metabolic functions, SMs (antibiotics and pigments) produced by microorganisms, specifically bacteria and fungus, are necessary [71]. The production of active SMs is facilitated by seven different metabolic pathways, which include the peptide pathway, hybrid pathway, nonribosomal polypeptide synthase pathway, b-lactam synthetic pathway, shikimate pathway, and carbohydrate pathway. According to earlier research, PGPRs connected to plant roots increase the production of SM in those plants when under stress [72–73]. In contrast to uninoculated plants that shield pea plants from dangerous diseases, Jain *et al*. [74] report that pea plants harbouring helpful bacteria, specifically *Bacillus subtilis* and *Pseudomonas aeruginosa*, produce higher concentrations of phenolic compounds and gallic acid. The results showed that the components found in roots are what improve the beneficial microbial communities around roots, which shield and strengthen plants' resistance against damaging soil microorganisms and other abiotic stressors [75–77].

1.6 Biological Control:

1.6.1 Natural Regulation:

The regular reduction of one or more microbes harmful activity using living agents is known as biological control [78, 79]. The biocontrol of soil phytopathogens that benefited from living things have been around for more than 80 years. It has been discovered that bacteria around roots are regarded as BCAs, which strengthen plants' defences against plant diseases [80]. Farmers have been using chemicals to quickly eradicate hazardous soil-borne diseases for the past few decades, but this chemical-based approach has resulted in environmental problems.

Alternatives to chemical and environmentally friendly methods have developed, such as biocontrol, which is now thought to be a viable method of controlling dangerous phytopathogens [81–85].

1.6.2 Biological Regulation:

The elimination of harmful effects from one or more biological researchers work to understand how BCAs combat dangerous pathogens and manage plant diseases so they might alter the conditions in the soil that are favourable for effective biocontrol or enhance existing biocontrol tactics [86]. To promote plant development while preserving wildlife and flora and to boost soil fertility, biocontrol actions are also used [87].

A. Beneficial microorganisms as agents of biocontrol against phytopathogens:

Fixing N_2, lowering hazardous chemical levels, promoting plant development and productivity, and controlling soil-borne phytopathogens are some of the positive functions of bacteria. Many beneficial bacteria genera are thought to be effective BCAs for managing plant illnesses brought on by bacterial, fungal, and plant parasitic nematodes (PPNs). The host plant and other nearby species were impacted by the effective use of BCAs to suppress nematodes and other detrimental microbiota. Applying *Pseudomonas* spp. increases the in vitro mortality of second-stage juveniles (J2s) of *Meloidogyne javanica* [88]. Using *Bacillus* isolates as a bioagent effectively reduces the number of root-knot nematode infestations in soil [89–91]. Tomato defence enzymes against root-knot nematodes are activated by *P. fluorescent* isolates [92]. Currently, phytopathogenic fungi cause more than 50% of losses to fruits and other crops at the postharvest period [93]. In the post-harvest stage, biocontrol of phytopathogenic organisms at the pre-harvest stage provides an effective substitute for pesticides against phytopathogens [94]. The biocontrol ability of *P. aeruginosa* against *Colletotrichum capsici*, the plant that causes anthracnose on chilli plants, was determined by Jisha *et al.* [95]. Additionally, P. aeruginosa causes the chilli plant to develop a systemic resistance to anthracnose. *Trichoderma* spp. is thought to be powerful BCAs among fungi, while other fungi with antagonism against a few fungal pathogens, such as Fusarium, *Alternaria, and Penicillium, as well as Gliocladium, Aspergillus, and Saccharomyces*, are also present. Of the fungus, *Trichoderma* spp. is thought to be strong BCAs, while additional fungi with antagonistic properties include Penicillium [96], Gliocladium [97], Aspergillus [98], and *Saccharomyces* [99].

It has been discovered that AM fungi activate genes linked to pathogenesis and SAR in inoculated plants, while nematophagous fungi use trapping structures to capture PPNs, such as root-knot nematodes [100, 101]. The most significant and effective BCA for PPNs is the nematodes egg-parasitizing fungus *Paecilomyces lilacinus*, which also offers a promising substitute.

B. Toxicity of heavy metals to the environment and human health:

The long-term industrial advancement and development has led to the acceptance of environmental contamination with heavy metals as a health risk [102, 103] for sustainable dwellings. Because of their enduring nature, heavy metals have long been recognised as potentially dangerous substances for human health. An important environmental problem, heavy metal contamination of agricultural soil can reduce plant productivity and the safety of products that are used as food and feed [104]. Using sunlight as their principal energy source, plants generate food. They absorb water from the soil ecosystem as well as beneficial nutrients and components. Occurring in organisms with physiological functions are iron, manganese, copper, cobalt, molybdenum, and vanadium. Moreover, organisms may experience varying degrees of toxicity from elevated levels of these metals [102]. Several additional elements, including lead (Pb), arsenic (As), mercury (Hg), and cadmium (Cd) have been accumulated and are considered highly dangerous [105]. Interaction between plants and microbes increases tolerance, resistance, and accumulation of heavy metals, which has significant effects on heavy metal detoxification [106, 107]. Microbes and plants employ a variety of defence strategies under stressful environments, such as complex formation, exclusion, release, and compartmentalization of metal-binding proteins such metallothioneins and phytochelatins [108, 109]. Using industrial wastes, waste disposal, agricultural intervention, and atmospheric deposition, toxic metals are released into the environment [110].

C. Role of beneficial microbes in detoxifying the heavy metals and plant growth enhancement:

Numerous microorganisms that live in soil have been identified as a possible aid in the remediation of contaminated environments. Rhizospheres are rich in microbes that fight off harmful pathogens and provide plants the power they need to create a defence system to ward against infections. Better polysaccharide and/or ganic acid synthesis is made possible by increasing the rhizosphere microbiota of plants, which improves metal solubility and gives plants a competitive edge during phytoremediation [111, 112]. Metal detoxification is regarded as a special class of pollution; however, wastewater treatment can be effectively treated at a reasonable cost by using phytoremediation technology [113]. Plants can withstand a variety of environmental toxins due to their special qualities, which include enzymes, antioxidant activity against reactive oxygen species, and biomass. Plants possess distinct features such antioxidant activity against biomass and reactive oxygen species, as well as enzymes, which enable them to withstand a wide range of environmental pollutants. For their function in the breakdown of metal, plant metal-binding protein-like genes have been identified from a range of microbes and plants, including Brassica, rice, maize, tobacco, soybean, and wheat [114]. There has been recent reporting on the efficacy of *Helianthus annus* L. phytoremediation in restoring industrial sites contaminated with heavy metals. *Zea mays, Erato polymnioides, Solanum lycopersicum, Hibiscus cannabinus, Paxillus involutus*, *Festuca arundinacea*, *Helichrysum italicum*, and *Poulus canescens* are additional plants that are appropriate for phytoremediation [115]. Some of the biochemical mechanisms involved in plant–microbe interaction and heavy metal uptake are translocation, chelation, volatilization, solubilization, precipitation, complexation, and immobilisation.

D. Importance of beneficial microbes for Sustainable agriculture and environment:

Roughly 2.4 billion people worldwide suffer from hunger as a result of the world's population growing at a pace of 1.05% year [116]. Synthetic pesticides are frequently employed to significantly increase crop yield to intensify agriculture to feed the entire world's population [117]. However, dangers including increased soil toxicity and salinity, soil hardening, noticeably decreased nutrient-carrying capacity, and waterlogging were made worse by the persistent and disproportionate use of pesticides [118]. Due to the resulting environmental disruption, farming methods that don't harm the environment must be used to supply the growing need for food. Consequently, efforts to create a sustainable agriculture paradigm were initiated. It is well acknowledged that microbes have immense potential in sustainable agriculture. The term "plant-microbiome" refers to the diverse microbial populations that live inside plants, such as bacteria, fungus, and archaea. Plant-microbiome interactions benefit plant survival and health without endangering the environment [119]. Thanks to technical advancements, the architecture of the plant-microbiome and its interactions with the host may now be investigated [200]. Microbes lived in various places on and within the plant body as endophytes or epiphytes [201].

The plant-microbiome interacts pleiotropically with the health of plants [202]. Microbes extend the life span of plants by enhancing immunity [205], preventing illness [204], and boosting health and yield [203–205]. Since site-specific bacteria increase crop longevity and production, they can be utilised as BCAs to reduce the environmental harm that pesticides cause. Do the bacteria have all the necessary characteristics for long-term viability development, notwithstanding their many benefits? There is still a need for agrochemicals that were once used. In an attempt to guarantee food security, they encourage crop output, yet they have a disastrous effect on our ecosystem and agricultural resources. Utilising the plant microbiome is necessary to strike a balance between environmental conservation efforts and rising food demand. Numerous plant microorganisms are already being employed in agriculture as long-term strategies for increased productivity [205].

This could be a useful substitute for environmentally friendly and sustainable crop production.

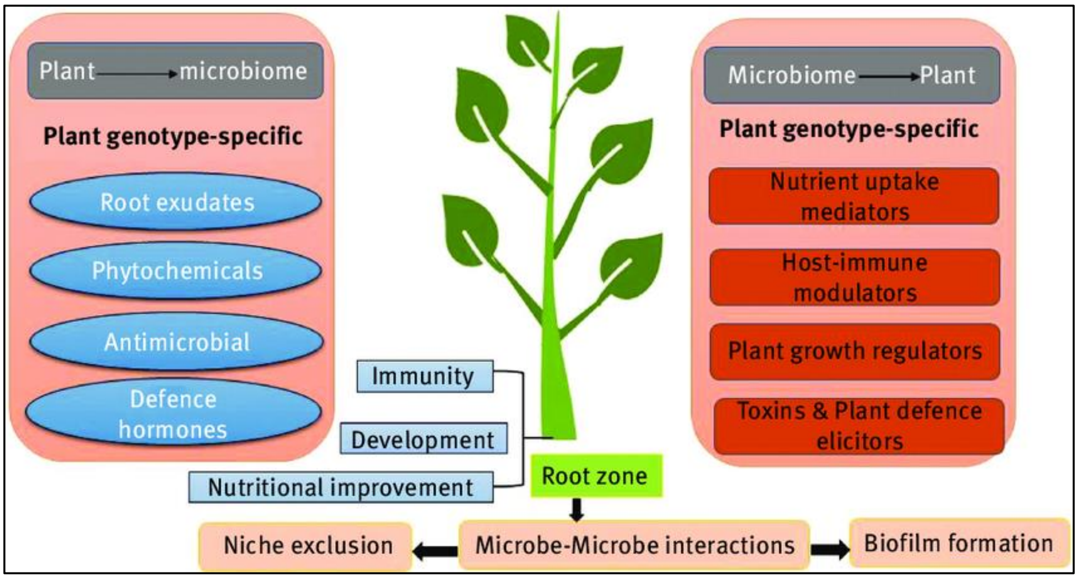

Figure 1.3: Beneficial features of microbes for plant growth and development.

1.7 Conclusion:

Currently, the biggest obstacle to meeting the world's food demand is food security. Plants have their built-in defence mechanisms to withstand a variety of obstacles. Different levels of plant-microbe interaction helped the plants create defence mechanisms against diseases, enhance nutrient uptake, and increase soil fertility.

In addition to various nutrients, plants also absorb complex harmful compounds from the soil environment known as heavy metals. These heavy metals can significantly impair crop yield and harm animal and human health. In numerous respects, PGPB and mycorrhizal fungi are acknowledged as helpful microbes that may counteract abiotic pressures without adversely affecting soil and groundwater resources.

Thus, the explanation of bioremediation mechanisms (microorganisms and plants) is the reduction or elimination of toxicants from the environment by biological resources. Much research has been done on the most recent developments in heavy metal bioremediation, and microbial-based heavy metals processing offers an environmentally acceptable alternative to the conventional method.

Beneficial microbes linked with plants affect the distribution and quantity of these microorganisms in plant tissues, and they also indirectly stimulate the production of biomass in the roots and shoots of plants. In addition, in order to mitigate or eradicate the harmful effects of heavy metals in the contaminated area, bioremediation requires the application of genetically modified bacteria with increased effectiveness. One innovative and affordable method for reducing abiotic pressure for environmentally friendly farming practices. We must investigate the whole range of applications for soil microbiome in order to counteract abiotic stress and improve plant development and growth, both of which can eventually support sustainable development.

Future Prospects:

Today's scientific community seeks to show how the microbiome protects the environment, enhances crop output, and improves plant health in order to achieve sustainable agriculture goals and lessen environmental stressors. The improvement of nutrient translocation, the health of the soil, and the detoxification of hazardous metals have all been demonstrated to be major benefits of plant-microbe interactions in increasing crop productivity.

The ability of microorganisms to control diseases, enhance plant health, and increase crop output has so far been observed and measured. We will be able to enhance the performance of microbes in various environmental settings and geographical places thanks to this understanding. It is necessary to create plans that include the knowledge currently available to formulate ecological concepts that, to achieve the ultimate objective of sustainable agriculture, can convert this knowledge into higher crop yield.

Under cooperative research programmes, government and policy makers should work to support newly established manufacturers and their products so that they can be used more extensively.

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