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Diversity of Soil Microbiome: Roles and Potential Applications

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ABSTRACT

Soil is a rich material containing lots of organic content, minerals, and microbial biodiversity. The microbes present in soil harbor capabilities of multitude importance, many of which are significant biotechnology wise as well. Production of antimicrobial compounds, plant growth promoting metabolites, a variety of enzymes, nitrogen fixation, and ability to bio-transform a lot of important compounds and to degrade a lot of toxic ones are just a few of the variety of functions that soil microbes can perform. However, only a small fraction of soil microorganisms can be cultured in laboratories due to the strict growth requirements of many microbes. To study these unculturable soil microbes, metagenomics is a helpful approach. This article discusses the importance of soil microbiomes, the roles they play for the soil health, as well as their potential applications.

1. INTRODUCTION

Soil is an unconsolidated natural organic material present predominately on earth's crust. It is a complex habitat for immense biodiversity responsible for the functioning and evolution of an ecosystem. It occupies one-third of all living organisms in an ecosystem (Paul, 2014). Microorganisms that inhabit soil have to devise some defense mechanisms to cope with different stresses such as moisture, temperature, exposure to chemicals, etc. Thus, different variable factors in soil are key determinants of persistent soil microbiota.

Microbiome is the totality of all microorganisms including bacteria, archaea, and fungi in an environment whilst microbiota is the total of all genomes of microorganisms present in a specific environment (Schlaeppli and Bulgarelli, 2015; Hao and Xiao, 2017).

Soil contains thousands of microbial taxa from all three domains of life. Every group has a tremendous contribution to the fertility and structure of the soil (Mendes *et al.*, 2013). More diversity is found in and around the rhizosphere as many nutrient exudates are released by plant roots, and in return, microbes there produce many plants growth-promoting metabolites such as phytohormones and siderophores. It has been reported in many studies that the rhizosphere contains more bacterial activity as compared to non-rhizosphere soil (Berendsen *et al.*, 2012; Prashar *et al.*, 2014). Soil microorganisms synthesize their own food by the breakdown of organic material present in the soil. In the process, they create humus, humin, and other polysaccharide-based substances. Humus plays a role in the water holding capacity of soil and also improves the texture and structure of the soil.

2. SOIL: AN EXCELLENT NICHE FOR MICROORGANISMS

2.1 Horizons of Soil

Horizons are distinct layering systems of soil characterized by physical and chemical properties. There are four horizons of soil which are O, A, B, and C, from top to bottom. The 'O (organic) horizon' is the topmost layer which mainly consists of undecomposed organic matter and can be easily distinguished into manure, plant and animal litter, and other organic matter. This horizon houses thousands of bacterial communities. Under this layer is 'A horizon' where plant roots and microorganisms are most active. This horizon is rich in mineral content and is darker in color. This layer is just beneath the topsoil and organic matter is present there as well. At the interphase between O and A horizons, the organic matter gets mixed with the mineral content resulting in "soil organic matter (SOM)". The next layer is the 'B horizon' which is less organic and more mineral in nature. It is derived from the parent material just under it and thus it has the least biological activity. Humic material can be found in this layer from the leaching of the above organic matter. Moreover, in the B horizon maximum illuviation, i.e., deposition or accumulation of silicate clays and of iron (Fe) and aluminum (Al) oxides is also found. The last is the 'C horizon' which is above bedrock or parent material and mostly contains rocks of the parent material. Here the microbiological diversity and biological activity is least found due to the scarcity of oxygen and organic material (Fierer, 2017).

2.2 Factors Responsible for Soil Genesis

Different factors play an important role in the formation of soil as proposed by Jenny (1983)

- 1) Climate, especially the temperature for the freezing and thawing cycles.
- 2) Geological formation of the bedrock.

- 3) Biological bodies such as plants as well as other soil-associated microorganisms including viruses, bacteria, fungi and archaea.
- 4) Topography of the soil is also important as it determines the nature of the soil.
- 5) Time, as it affects the differentiation of soil.

2.3 Factors Determining the Soil Microbial Communities in Soil

Soil microflora is greatly affected by the conditions of soil in which they are present. For example, it has been suggested that as moisture content in soil is depleted, decomposers present in the soil also start to diminish (Manzoni *et al.*, 2012). The following biotic and abiotic factors can have synergistic effects on the microbial composition of soil (Fierer, 2017):

- a) pH of the soil
- b) Soil moisture content
- c) Availability of carbon and its quality
- d) Nitrogen and phosphorus content
- e) Soil texture and structure
- f) Temperature of the soil

3. WORLD OF SOIL MICROFLORA

3.1 Characteristics of Soil Microbiome

All taxa of microbes are not equally abundant in soil. It depends on the properties of the soil as well as biotic and abiotic parameters. Moisture content is one of the prominent factors for total soil biomass. As moisture increases in soil, its microbial composition tends to become more diverse. Among soil microbiomes, bacteria and fungi are most dominant constituting 10^2 - 10^4 times the biomass of the soil as compared to others. Among these two, different studies on soil profiling have suggested that bacteria are the most dominant ones in soil microbial communities (Hakeem *et al.*, 2016). In one of the studies conducted by Chao (2012), it was reported that the bacteria are in dominant numbers as compared to fungi in tomato-grown



soil. They also reported that as the depth of the soil is increased, the abundance of fungi and actinomycetes starts declining. Following is a brief account of the most dominant microorganisms found in soil.

3.1.1 Archaea

These are thought to be the most ancient microbes. They are normally present in extreme environments such as marshes and hot springs. Instead of peptidoglycan, proteins and polysaccharides are present as a component of the archaeal cell wall. Their cell membrane is adapted to tolerate harsh environments by having branched chain fatty acids. Methanogens, halophiles, thermophiles, and other extreme microorganisms are examples of archaea (Kaviya *et al.*, 2019).

3.1.2 Bacteria

Soil bacteria play an important role in the establishment of biogeochemical cycles. They are present in microsites found among the soil particles. Most residing soil heterotrophic bacteria are *Acinetobacter*, *Agrobacterium*, *Bacillus*, *Caulobacter*, *Hyphomicrobium*, *Alcaligenes*, *Micrococcus*, *Sarcina*, *Streptococcus*, *Xanthomonas*, *Pseudomonas*, *Metallogenium*, and *Flavobacterium* while autotrophic bacteria include nitrifiers, *Thiobacillus* and others (Harter *et al.*, 2008). Many bacteria, known as plant growth promoting rhizobacteria (PGPR), promote plant growth by inhabiting around roots of the plants and include *Arthrobacter*, *Azotobacter*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Pseudomonas*, *Serratia*, and *Streptomyces* spp. (Gray and Smith, 2005; Dimkpa *et al.*, 2009). Bacteria are involved in accelerating a variety of physical and biochemical processes in soil which ultimately promote plant health and growth. PGPRs directly promote the growth of plants by providing fixed nitrogen, soluble phosphate, iron, and phytohormones. Many processes important to the health of plants are

carried out by bacteria. For instance, *Bacillus* and *Pseudomonas* are known to be involved in ammonification and convert organic nitrogen into ammonia. In nitrification, *Nitrosomonas* and *Nitrobacter* play an important role by converting present ammonia into nitrite. Denitrification involves *Achromobacter*, *Bacillus*, *Pseudomonas* and *Micrococcus*. Bacteria such as *Azotobacter*, symbiotic *Rhizobium*, *Bradyrhizobium* and *Beijerinckia* play pivotal role in nitrogen fixation (Lenart-Boroń and Boroń, 2014).

Many PGPRs are also known to reside inside the roots of plants in the form of root nodules. These are sometimes called as iPGPRs (internal PGPRs) as compared to ePGPRs (external PGPRs) that live outside the plants. Soil is also abundant with bacterial species including *Burkholderia terrestris*, *B. humi*, *B. udeis*, *B. choica* and *B. telluris* (Vandamme *et al.*, 2013).

Cyanobacteria are abundantly found in moist soil and aquatic environments where they act as nitrogen-fixing organisms. They can be heterocystous and non-heterocystous. Heterocystous cells are produced under nitrogen fixing conditions. Abiotic factors e.g. temperature, pH, and moisture content affect the diversity of cyanobacteria in the soil. All varieties of cyanobacteria, such as unicellular, filamentous and colonial, are found in soil (Imadi *et al.*, 2016).

3.1.3 Actinomycetes

This group of bacteria is found naturally in soil. They have long, branched hyphae and their mycelium is 0.5-1.2 µm in diameter. They grow abundantly in soil irrespective of nitrogen concentration. They are producers of many antibiotics such as terramycin, aureomycin, cycloheximide, chlortetracycline, oxytetracycline, chloramphenicol, streptomycin, and neomycin. They are also important in increasing soil functionality by the



production of lipases, xylanases, and pectinases (Suneetha and Khan, 2010).

3.1.4 Fungi

Arbuscular mycorrhizal fungi are the most dominant fungi present in the soil where they form mutualistic ectomycorrhizal associations with plants, providing nutrients to the host and thus improving the growth and development of the plant. Fungi are one of the most important groups of microorganisms and contribute to the ecosystem as decomposers, mutualists, and symbionts (Taylor *et al.*, 2014). Almost 90% of plants are in symbiotic relationship with soil fungi (Miransari, 2011). Fungi are major decomposers of the soil organic matter and thus help in the maintenance of soil structure. One of the important genera of soil fungi is *Aspergillus*. *Aspergillus* and *Penicillium* species are most dominant due to their defense mechanisms; *Aspergillus* produces toxins and penicillin is produced by *Penicillium* which inhibits the growth of other microbes in the surrounding environment (Sharma and Raju, 2013).

4. FUNCTIONS OF THE SOIL MICROBIOME

Soil microbiome contributes greatly not only to soil structure and function but also to the ecosystem. The most important one is perhaps the decomposition and recycling of organic matter leading to increased soil fertility. Soil microbiome also affects the soil structure as they produce substances such as polysaccharides and mucilage which contribute to aggregation of soil particles. The presence of fungi in the soil is known to increase the water retention capacity of the soil. Soil microbiome plays an essential role in the carbon cycle which results in the availability of organic carbon for plants (Johns, 2017). Soil microbes can consume as well as produce atmospheric gases such as carbon dioxide, hydrogen, nitric oxide, nitrous oxide, methane,

and other volatile organic compounds by H_2 oxidation, CH_4 oxidation, and nitrogen reduction (NO , N_2O , and N_2), contributing to the soil health (Fierer, 2017).

Microbes have several metabolic processes that convert organic phosphorus into inorganic form through mineralization. This helps the plants to uptake phosphorus more readily. Organic acids, such as glycolic acid, formic acid, succinic acid, and acetic acid, produced by many bacteria such as *Bacillus* and *Pseudomonas* species, have been reported to be helpful in the mineralization of phosphorus (Chalot *et al.*, 2002). Microbial phosphatases such as nucleotidases, sugar phosphatases, nucleases, and phospholipases also have great contribution in the phosphorus cycle (Dick *et al.*, 2000).

One of the most important functions of soil microbes is the nitrogen fixation. This can be carried out by the symbiotic relationship of *Bradyrhizobium* and *Rhizobium* with leguminous plants. Asymbiotic aerobic bacteria such as *Azotobacter* and *Beijerinckia*, and anaerobic bacteria such as *Clostridium*, and free-living photosynthetic cyanobacteria are also known to fix nitrogen (Zehr and Capone, 2020; Schulte *et al.*, 2021).

4.1 Role in Soil Health

Soil health can be determined by many indicators. The biological indicators include respiration, cofactors secondary metabolites formation, nutrient cycling and other microbial activities. Soil health can be referred to as soil fertility, and it is one of most important feature of soil ecosystems. Soil structure also contributes to the soil health. Soil health depends on interaction between different processes, and microbial activity is one of them (Frąc *et al.*, 2018).

Soil microbiome constitutes the biosphere which is involved in nutrient cycling that tends to maintain the soil fertility. The use of recent



technologies of agriculture and heavy machinery has resulted in extensive cultivation in many areas, without enriching the soil. The overuse of land damages the soil structure and fertility, and in short time cultivatable area can be turned into uncultivable. One cm of topsoil formation takes about 300 years but the rate of loss of soil due to erosion is much higher. Biological activity of soil microbiomes maintains the physical and chemical characteristics of soil. According to the soil scientist Dr. Elaine Ingham, “If we lose both bacteria and fungi, then the soil degrades”. The bacteria, fungi, and algae associated with rhizosphere enhance soil health and protect plants from many soil borne diseases (Jamir *et al.*, 2019; Sabale *et al.*, 2019).

4.2 Role of Microbial Enzymes in Soil Health

Bacterial extracellular and intracellular enzymes can be used as soil quality indicators. For instance, beta-glycosidase enzyme has an active role in degradation and hydrolysis of beta-glycosides present in the decomposing organic matter. Biological activity of soil can also be predicted by dehydrogenase enzyme which is also involved in organic matter transformation (Jamir *et al.*, 2019). Chitinase enzyme also reflects the soil health by biodegradation and hydrolysis of chitin to control soil-borne diseases. Hydrolysis of sulphate esters in soil are catalyzed by aryl-sulphate sulfotransferase which is produced by the soil bacteria. These all have the ability to recycle organic matter in the soil (Sabale *et al.*, 2019). It is assumed that in phosphorus cycle the enzyme phosphatases plays a major role. When there is a deficiency of phosphorus in soil, phosphatase enhance the recycling of phosphorus (Versaw and Harrison, 2002). Alkaline phosphatase is mainly produced by bacteria that are also involved in phosphorus cycle. The enzymes amylase and urease are

also involved in nutrient mineralization (Jamir *et al.*, 2019).

Many soil microbes produce enzymes which are involved in the degradation of pesticides and other toxic substances present in soil. This helps retain soil fertility and promote biological activities. For instance, pentachlorophenol is used as pesticide, and is known to persist in the soil. Many fungi such as *Phanerochaete chrysosporium*, *Antracophyllum discolor*, *Trametes versicolor*, *Ganoderma lucidum*, *Armillaria mellea*, and *Gloeophyllum striatum* have been reported to have the ability to degrade and mineralize PCP (Malik *et al.*, 2017).

4.3 Role of Fungal Biodiversity in Soil Health

In the past few years, researchers have been emphasizing the potential applications of cultivating soil fungal biodiversity to improve soil quality and health for better production of crops (Ramachandra *et al.*, 2018). Fungi take part in breakdown of organic matter and hence release nutrients for soil health and plant devolvment. Many fungal species are also reported to play important role in plant protection against pathogenic microbes (Frąc *et al.*, 2015). Arbuscular mycorrhizal fungi are also involved in enrichment of nutrient cycle, improvement of soil structure and soil quality, increased uptake of low mobility ions (Frąc *et al.*, 2015).

Studies show that addition of chitin to the soil increase soil microbiome community that is essential in suppression and degradation of pathogenic fungi. It can be used as a good alternative to fungicides that tend to destroy useful microbes and have negative effect on the soil health (Goss and De Varennes, 2002).

4.4 Nitrogen Cycling for Soil Health

Traditional methods of agriculture employ chemicals such as fertilizers, herbicides to improve the NUE but this could affect the soil



health and biodiversity. Physiochemical approaches are made to decrease the loss of nitrogen from soil by utilizing the structure and activities of soil nitrogen cycling of microorganism (Hu *et al.*, 2017). Recent advances in metagenomics has revealed that soil microbes such as nitrogen fixing bacteria, ammonia oxidizing bacteria, ammonia oxidizing archaea, nitrate oxidizing bacteria, and DNRA (Dissimilatory Nitrate Reduction to Ammonium) bacteria play an important roles in biogeochemical cycling of nitrogen for the fertility of soil (Hu and He, 2018). By manipulating these microorganisms we can cause reduction in nitrification and denitrification pathways that lead to loss of nitrogen and can upregulate the DNRA pathway capable of reserving N in soil; resulting in multiple benefits such as soil fertility, less use of fertilizers, increase crop production and less NO₂ emission (Gao *et al.*, 2017).

4.5 Role in Plant Health

Conventional agriculture methods make use of synthetic fertilizers and pesticides to meet the food demand. However, these synthetic additions effect soil and plant health. Recent studies have focused on understanding of relationship between soil microbial community and plants by using soil metagenomics. A lot of research his being done to understand and exploit the beneficial role of soil microbiome for sustainable agriculture (Misra *et al.*, 2017). Plant vital attributes such as growth and health, protection against phytopathogens is increased by manipulating bacterial microbiome and bioinoculants. These methodologies eventually decrease the use of synthetic fertilizers (Adesemoye and Kloepper, 2009). Microbiome of soil linked with rhizosphere plays an important driving force of fundamental metabolic processes that contribute to plant growth producing hormones, protection against disease causing

pathogens, and stress response. Complex relationship occurs at root exudates and they act as substrate and signaling molecules for microbes (Sabale *et al.*, 2019).

4.6 Role of PGPB or PGPR in Plant Health

Studies show that PGPB are capable of influencing plant growth and health either directly or indirectly (Santoyo *et al.*, 2016). Many of them are known to produce exopolysaccharides leading to soil aggregation, plant fitness and water stability. PGPB promote plant growth by facilitating the uptake of water and necessary nutrients such as iron, nitrogen, and phosphorus along with regulating the level of plant growth hormones such as cytokinins, auxins and gibberellins (Calvo *et al.*, 2017). For example, *Bacillus subtilis* strains have been used as PGPB for phosphate solubilization. *Rhizobium leguminosarum* is involved in regulation of cytokinins and auxins (Jamir *et al.*, 2019).

It was established that for plant fitness and metabolism iron is an essential nutrient. Studies show that in iron depleted environment, soil microbes produce certain low molecular weight organic compounds called siderophores (the metal-chelating agents) which promote the growth of plants and enhance their yield by increased iron uptake. For instance, *Pseudomonas stutzeri* is known for this ability (Saha *et al.*, 2016). Fluorescent pseudomonads are also known to produce siderophores having high affinity for iron (Lareen *et al.*, 2016). Experimental plants grown in the soil enriched with pyoverdine siderophores produced by fluorescent *Pseudomonas* spp., enhanced iron levels were observed in the plants. Another research conducted on plant-promoting activities of fungi revealed that in chickpea plants, roots and shoots length are increased by siderophores produced by *Aspergillus Niger*, *Penicillium citrinum*, and *Trichoderma harzianum* (Saha *et al.*, 2016).



Some PGPB are photostimulators and produce phytohormones that stimulate plant growth and health. For instance, phytohormone ethylene level can be reduced by PGPB such as *Pseudomonas* sp. (A3R3, RJ15), *P. aeruginosa*, *P. fluorescens* and *Burkholderia cepacia* by producing enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase; that cause breakdown of the compound ACC which is the precursor of ethylene in higher plants (Glick, 2012). Studies have shown that plants that interact with the variety of PGPR are capable of increased photosynthetic activities, drought and salt tolerance (Wallenstein, 2017). Treatments combined with PGPR are more effective in disease suppression than either alone. For example, PGPR, mycorrhizal fungi, and 50 % fertilizer treatment to soil induced greater production than by using 100% fertilizer. This helps in the better absorption of nitrogen and phosphorus. Other research reveals that by using compost in combinations with beneficial microbes elevate the ability of plants to suppress pathogens (Wallenstein, 2017).

4.7 Role of AM Fungi in Plant Health

In most plant species, a major group of mutualistic symbionts consist of *Arbuscular mycorrhizal* fungi that are known for establishing association with plant roots (Johnson, 2010). It plays a crucial role in plant health and development by enhancement of nutrient acquisition and recycling in soil that also improves soil structure. It also plays an important role in forest ecosystem. Manipulating the combinations of PGPRs and AM fungi is a very beneficial biotechnological approach in supporting new trends in agriculture (Jeffries *et al.*, 2003).

4.8 Biofertilizers for Plant Health

Biofertilizers are also called as microbial inoculums. Research in the field of phyto-beneficial microorganisms has resulted in the

progressive development of different bio-fertilizers that can fulfill crop nutritional requirement (Jamir *et al.*, 2019). Some of the important soil bacteria such as *Azospirillum brasilense* and PGPR are used in biofertilizers. Biofertilizers play an important role in soil manageability and sustainability, promoting plant growth by providing nutrients in addition to nitrogen fixation, solubilization of phosphate, along with protection against pests and diseases (Jamir *et al.*, 2019).

4.9 Increasing Plant Resistance Against Biotic and Abiotic Factors

Abiotic and biotic stress cause damage to plants and cultivated lands leading to lower yield of the crops. Soil microbiome, due to its uniqueness, genetic capabilities and being able to tolerate extreme conditions, play a crucial role in stress management of plants. This is because of their metabolic abilities to severe in harsh environmental conditions. Research in soil metagenomics is the gateway to understand this uniqueness of microbes and how this ability can be manipulated to attain maximum crop yield.

Biotic stress factors include the infectious pathogens. Soil bacteria such as *Achromobacter*, *Azospirillum*, *Bacillus*, *Burkholderia*, *Enterobacter*, *Methylobacterium*, *Microbacterium*, *Paenibacillus*, *Pantoea*, *Pseudomonas*, *Rhizobium*, and *Variovorax* spp. are reported to build tolerance in plants against different abiotic stress factors (Meena *et al.*, 2017).

4.10 Resistance Against Biotic Stress Factors

Abiotic stress factors include temperature, humidity, light intensity, water, nutrients and CO₂ management. These factors are necessary for plant growth and health. If any of these factors is disturbed or altered, it can affect plant growth. Research has shown that PGPR also



have a role as the bioprotectants for the plants, leading towards improvement in plant resistance capabilities. Study shows that *Pseudomonas aeruginosa* has the ability to withstand both biotic and abiotic stress factors (Pandey *et al.*, 2012). *P. fluorescens* MSP-393 used has the ability to overcome salt stress by producing osmolytes and salt stress induced proteins (Paul and Nair, 2008). With the help of such PGPR, plants detect and react towards abiotic factors by changing level of different phytohormones, defense related proteins and enzymes, antioxidants and epoxy polysaccharides (Choudhary, 2012).

Some PGPR synthesize phytohormones like abscisic acid, gibberellins, ethylene, auxins, cytokinins and brassinosteroids which control various physiological and biochemical processes that promote cell growth and division, and help plant to bear environmental stress (Fahad *et al.*, 2015). Salinity results in decreased level of phosphorus which results in phosphorus deficiency symptoms in plants. Certain species of PGPR such *Pseudomonas*, *Erwinia*, *Rhizobium* and *Bacillus* are involved in conversion and solubilization of insoluble organic phosphate compounds (tricalcium phosphate, rock phosphate) to the form which is utilized by the plants (Rodríguez and Fraga, 1999).

In water deficient conditions the amount of ROS increases in plant tissues. It was observed that Medicago plants associated with IAA overproducing PGPR, higher antioxidant activity was observed which enhanced plant safety against salt stress and oxidative damage by scavenging ROS (Carmen and Roberto, 2011). A study showed that by manipulation and combination of AM fungi and nitrogen fixing bacteria; legume plants observed to overcome drought stress. One study showed that proline accumulation is increased in plant leaves which are suffering with drought and salt; soil bacteria *Bacillus subtilis*, *Rhizobium* and *Pseudomonas* are involved in production

of higher level of free proline. This tends to increase plant tolerance against osmotic stress with low electrolyte leakage, water maintenance in leaves and selective uptake of potassium ions. Recent research in soil metagenomics has reported the potential role of PGPRs in conferring resistance to water stress in tomatoes and peppers plants (Jamir *et al.*, 2019).

In the *Rhizobium*, the Trehalose metabolism plays major role in plant growth, yield and tolerance against abiotic stress. *Achromobacter piechaudii* ARV8 produces 1-aminocyclopropane-1-carboxylate (ACC) deaminase enzyme. It was reported that plant ACC is degraded by bacterial cells to provide nitrogen, energy and show systematic tolerance against drought and salt stress, and suppression of ethylene stress in tomato and pepper plants (Glick, 2012).

Actinobacteria are the most common soil bacteria. It was reported that *Streptomyces rochei* SM3 triggers the ET-mediated defense pathway (Ethylene-mediated defense pathway); produces ACC deaminase that reduces ACC levels in plants by activated phenyl propanoid pathway, that ultimately overcomes the salt stress. Under salt stress, these bacteria were found to significantly increase in chlorophyll content of plants and plant biomass and caused reduction of proline in leaves which helped to increase resistance of plants against these abiotic stresses. *Streptomyces pada* AOK-30 is known to help plants resist drought by modification of cell wall structure, increase accumulation of callous and cell wall lignification's of sieve cells under high osmotic pressure (Prathyusha and Bramhachari, 2018). *P. putida* Rs-198 helps to cope with alkaline and high salt stress by increasing the uptake of potassium, calcium and magnesium and decrease absorption of sodium. This leads to plant growth and increased germination rates (Yao *et al.*, 2010).



Piriformospora indica is important and unique fungal specie that establish symbiotic relationship with plants and show positive interactions with different agricultural and horticultural plants. This enables plants to grow under severe nutrient stress conditions. The fungus enhances plant growth and development even if they are grown in nutrient deficient soils and provide them resistance against abiotic stress (salt, drought, water, chilling, high temperature and heavy metals), biotic stress (root and foliar pathogen), promote early flowering and increase seed production (Johnson *et al.*, 2014).

4.11 Reduction Against Biotic Factors/Diseases

Recent advances in metagenomics have provided new tools to analyze soil borne microbes. Innovations in this field can help to provide strategies to reduce pathogenic diseases in plants. The application of many soil microbes in fact is a cost-effective method of increasing plant resistance to insects and pests. Certain PGPB act as biopesticides, which reduce the plant damage, or the deleterious effect caused by harmful fungi and bacteria. They inhibit the growth of the pathogens by production of antibiotics for example 2,4-diacetylphloroglucinol, antifungal metabolites, siderophores, by competition and lytic enzyme secretion. For example: *Burkholderia* sp. used as PGPR and its mode of action is siderophores formation (Schlatter *et al.*, 2017; Del Carmen Orozco-Mosqueda *et al.*, 2018).

Bacillus subtilis GBO3 can start defense related pathways through salicylic acid and jasmonic acid. *B. amyloliquefaciens* 937b and *B. pumilus* SE-34 provide immunity against tomato mottle virus. Furthermore, PGPR have been found to be effective against spotted wilt virus in tomatoes as well (Bhardwaj *et al.*, 2014). Study reveals that barely plants inoculated with fungus *Piriformospora indica* showed tolerance

against *Fusarium* and *Blumeria* infections (Coleman-Derr and Tringe, 2014).

Volatile antibiotics, produced by many bacteria, include sulfides, ketones, aldehyde, and HCN. Non-volatile consists of polyketides, phenylpyrrole and pyrrolnitrin. *Bacillus subtilis* secretes various lipo-peptide antibiotics e.g. surfactin, zwitter-micina, iturin and bacillomycin to protect from plant pathogens. *F. oxysporum* plays a major role in reducing occurrence of diseases. Soil borne diseases can effectively be suppressed by fluorescent pseudomonads that have tendency to form 2, 4 - DAPG, known for this suppression activity (Attwood *et al.*, 2019). Phytopathogenic fungal growth can be controlled effectively by bacterial enzymes known as lytic enzymes; the typical examples of which are glucanases, proteases, celluloses and chitinases (El-Tarabily, 2006). One study showed that in verticillium wilt disease in wheat caused by the fungal plant pathogen *Verticillium dahliaekleb*, soil bacteria *Bacillus subtilis* showed effective reduction in disease by suppression and enhanced uptake of bioorganic fertilizer. *Bacillus subtilis* produces a variety of fungicides; and its several strains were observed in effective disruption of the fungal cell wall (Luo *et al.*, 2010). Crop diseases can also be controlled by different fungi such as *Glomus* and *Trichoderma* that suppress the effect of fungal pathogens (De Coninck *et al.*, 2015). *Beauveria bassiana* and *Metarhizium anisopliae* are also involved in plant growth and pest or insect resistance (Pineda *et al.*, 2017). Production of siderophores is reported to reduce iron availability for the pathogens by binding tightly to iron. This decreased availability of iron start killing the pathogens, e.g. plant pathogen *Erwinia carotovora* is affected by the siderophores production by various plant growth-promoting *Pseudomonas fluorescens* strains (Wei *et al.*, 1991).



Pyoverdine siderophores produced by pseudomonads play important role in biocontrol of *Fusarium Oxysporum* which cause wilt disease in potato plants. They are also known to suppress phytopathogens in peanut and maize plants (Lewis *et al.*, 2010). *Bacillus subtilis* is also known for the control of *F. Oxysporum* (Saha *et al.*, 2016). Scientists have reported that fungal pathogens like *Phytophthora parasitica*, *Pythium ultimum*, and *Sclerotinia sclerotiorum* can be killed or suppressed by the inhibiting their growth by certain PGPB siderophores (Saha *et al.*, 2016).

4.12 Novel Molecules of Industrial Importance

Research in soil metagenomics has revealed many novel enzymes, molecules and biocatalysts. Metagenomics is currently considered as one of the most appreciated technologies to provide these novel molecules for industrial applications at large scale productions. Manipulation of these molecules for industrial importance directly from soil microbiome is more efficient method than traditional method of cultivation of these microorganisms. There are various molecules and compounds are produced by soil microbes which are used in different industries e.g. textile, food, cosmetics, pulp and pharmaceutical industries.

4.13 Novel Enzymes

One of the most important industrial enzymes is cellulase which is produced by different soil-borne microbes. Recently it has been isolated by utilizing metagenomic techniques of constructing libraries followed by purification of biologically active clones. Cellulases are used in food industry for processing of juices and in baking. It is a major component of animal feed that enhance nutritional qualities. It also has a role in de-inking of paper (Nazir, 2016).

Lipases enzyme are universal carboxyl esterases that catalyze the hydrolysis and synthesis of relatively long chain acyl glycerols. Lipases are widespread in soil microbial communities including fungi and have primary importance of potential application in industry especially as detergents for oil and fats degradation, dairy, drug manufacture, paper and biodiesel production. A metagenomic study reported isolation of lipase stable at high temperature 35-60°C. Metagenomic libraries were constructed using oil-contaminated soil and was expressed in *Pichia pastoris* GS115 (Zheng *et al.*, 2013). Verma *et al.* (2013) reported isolation of xylanase through metagenomics of compost soil. The enzyme showed high alkaline stability, thermo-stability. A thermostable and calcium dependent amylase is isolated from soil through metagenomics (Vidya *et al.*, 2011).

A novel cold-adapted esterase was isolated from unculturable soil microbes using metagenomics. It can be activated under wide temperature range even at lower temperatures. Cold active esterases have potential industrial applications such as additives in laundry detergents for cold washing and catalysts for organic syntheses of unstable compounds at low temperatures and in food processing (Ko *et al.*, 2012).

Lignocellulolytic enzymes isolated from soil bacteria and fungi have potential applications in industries, in biorefineries and ethanol production. Laccase, a lignolytic enzyme, has important role in food, chemical and cosmetic industries. In this era there is increased need of such enzymes for bioconversion of agricultural sources and in ethanol production (Sette *et al.*, 2008).

4.14 Enzymes and Genes of Pharmaceutical Importance

Recent studies on soil microbiome reveal several uncultured bacteria and fungi involved

in antibiotic production. A clone of soil metagenomic library was found synthesizing deoxy violacein and the broad spectrum antibiotic violacein. Another one was found to produce long chain N-acyl tyrosine antibiotics (Ghazanfar and Azim, 2009). Many natural antibiotic resistant genes are found in agriculture soil samples. By construction of metagenomic library and screening, clones showing resistance to antibiotics such as tetracycline, chloramphenicol, kanamycin, minocycline, gentamicin, amikacin, amino glycosides, streptomycin and rifampicin have also be identified (Su *et al.*, 2014).

In a study, cluster of genes “*bor*” have been reported from soil that encodes indolotryptoline based compounds; a family of natural products that have potential activity against specific tumor cell lines. Screening of soil metagenomic libraries has also reported novel amidases. Amidases are involved in the production of β -lactam antibiotics and novel *Penicillium* acylase (Gabor *et al.*, 2004). Research also reveals soil microbes that have specific genes to encode vitamins such as biotin. Hence manipulation of these novel enzymes and compounds can aid pharmaceutical industry to increase their productivity (Entcheva *et al.*, 2001).

4.15 Bioremediation

Advance research in metagenomics of soil and next generation sequencing has played a crucial role in understanding the genetic variability, composition and metabolic processes of microbiome which aid in degradation and detoxification of organic and inorganic pollutants that contaminate the soil. These soil contaminations are due to rigorous industrialization, large scale disposal of manufacturing waste, leakage of organic compounds, pesticides, chemical fertilizers and oil spills. These environmental stressors are causing antagonistic effect on ecosystem. Recent advancement in the process of

bioremediation of these pollutants has been by manipulation of metabolic and enzymatic activities of eco-friendly and beneficial microbes (Lorenz and Eck, 2005).

Soil bacteria and fungi produce various microbial enzymes which are involved in degradation of harmful pollutants. This strategy of bioremediation is cost-effective. Many microbes are involved in degrading deadly hydrocarbons. Many rhizospheres' microbes are involved in biosurfactant production which helps in bioremediation of soil. These biomolecules are actively used as an alternative of harmful, persistent surfactants (Sabale *et al.*, 2019). Rhizo-remediators help in detoxification of organic pollutants and show improvement of bioaugmentation (Misra *et al.*, 2017).

The utilization of PGPRs in rhizo-remediation seems to be effective. Inoculation of PGPRs in the contaminated soil promotes plant growth via rhizo-remediation by production of IAA, nitrogen fixation, solubilization of P and producing siderophores. PGPRs and AM fungi have been used in nutrient poor soil to increase remediation of heavy metals. The application of PGPRs strains decrease the toxicity of pollutants resulting in better growth of plants even in heavy metal contaminated soil. PGPR are also involved in recycling of nutrients and detoxification of chemicals as well as pesticides (Bhattacharyya and Jha, 2012). It is reported that certain rhizobacteria associated with *Alyssum murale* support plant growth and health by decreasing nickel toxicity. Siderophores produced by PGPR can be utilized as environmentally friendly agent for the remediation of heavy metals (O'brien *et al.*, 2014). The production of Siderophores by the *Pseudomonas azotoformans* aids in remediation of arsenic from the contaminated soil. 54 percent arsenic remediation has been reported by *Agrobacterium radiobacter* associated with siderophores. *Pseudomonas fluorescens* produces siderophores that are



involved in mobilization of various metals such as Fe, Ni, and Co. *Pseudomonas* species isolated from soil compost is reported to scavenge zinc and thus acts as zinc bioremediation agent (Mehri *et al.*, 2012).

PGPR can also be effective in saline soil through photo-remediation and promote plant growth. These are also reported to enhance salt uptake by plants, thus reducing salt concentration in soil. Study shows that cyanobacteria *Nostoc ellipsosporum* HH-205 and *N. punctiforme* HH-206 isolated from salt effected areas are also involved in bioremediation of salt (Fahad *et al.*, 2015).

Laccases produced by *Theiophoraterrestris*, *Marinomonasmediterranean* breakdown the reduced phenolic and aromatic substrates. *Bacillus thuringiensis* and *Klebsiella* Sp. produce hydrolytic enzymes and are involved in hydrolysis of organic pollutants by bond cleavage that reduce the toxic effect of compounds (Karigar and Rao, 2011).

Bacteria *Flavobacterium* sp. form *Phanerochaete chrysosporium* produce oxidoreductase enzymes and are involved in remediation of many toxic organic compounds. Oxygenase syntheses from *Methylosinus trichosporium*, *Bacillus subtilis* helps in remediation and detoxification of organic pollutants. *Bacillus sphaericus* is involved in the production of peroxidases that catalyzes oxidation of organic and inorganic compounds (Kumar and Sharma, 2019).

Research has shown that bioremediation is most effective by manipulation of two techniques. First bioaugmentation involved in the introduction of designed microbial population which has catabolic potential for the degradation of pollutant. E.g. degradation of 3, 5-dinitrobenzoic acid (3, 5 - DNBA) was enhanced by manipulating microorganism like *Comamonas testosteroni* A3 and *Pseudomonas putida* M9 (Paliwal *et al.*, 2012). Second strategy is the bio-stimulation that enhances the

local microbial population by increasing the nutrients. A report shows that combination of bio-stimulation via soil amendment with 300 ppm of phosphate and inoculation with killed recombinant *E. coli* cells compressing atrazine chlorohydrolase showed successful bioremediation of soil contaminated with high level of herbicide atrazine (Rayu *et al.*, 2012).

4.16 Potential Use in Medicine

Microbiomes are also being explored for their potential as clinical biomarkers, therapeutics, and personalized medicine. Microbes compete for survival, and while resisting biotic and abiotic factors, they develop abilities of defense, attack and signaling, which aid in the development of potential new drugs. Microbes like Actinomycetes, Bacilli and filamentous fungi have ability to produce secondary metabolites and have the potential for the drug discovery beneficial for infectious, central nervous system and cardiovascular diseases (Demain and Sanchez, 2009).

Biapenem is produced by *Streptomyces cattleya* and have antibacterial mode of action against anaerobes. Likewise, Deptomycine produced by *Streptomyces raseosporus* and Telithromycine produced by *Saccaropolyspora erythraea*. Everolimus and Mycophenolate sodium are synthesized by *Streptomyces hygroscopicus* and *Penicillium brevicompactum* and have to potential to be immunosuppressants (Singh and Macdonald, 2010).

Several soil microbes are involved in production of anti-cancer drugs which are approved by FDA for therapeutic utilization. Bleomycin anticancer agent produced by *Streptomyces verticillus*, Daunorubicin (daunomycin) by *Streptomyces peucitius*, Doxorubicin hydrochloride (adriamycin) by *Streptomyces peucitius*, Pentostatin by *Streptomyces antibioticus* and fungus *Aspergillus nidulans*, Streptozocin by



Streptomyces achromogenes, Mithracin by *Streptomyces argillaceus*, Mitomycin C by *Streptomyces verticillatus* and Actinomycin D is synthesized by *Actinomyces* spp. (Pettit, 2004).

Medical bioremediation comprises of the treatment of different metabolic conditions using microbial enzymes. Researcher thought that catabolic insufficiency is the major reason of aging, and elimination of certain metabolic products that accumulated intracellularly reduced the symptoms of certain disease and aging. For example, 7-ketocholesterol is associated with Alzheimer's disease and atherosclerosis and has cytotoxic properties. Studies show that if its concentration is reduced the progression of disease slows down. Certain bacteria which are involved in mineralization of 7-ketocholesterol have been isolated. Additionally, *Mycoplasma hyorhinis* and *Mycoplasma penetrans* were observed in degradation of amyloid-beta and neurofibrillary tangles also associated with Alzheimer's disease (Zhao *et al.*, 2008).

Organophosphate (OP) compounds are widely used in pesticides and are highly toxic. Approximately three million poisoning and 300,000 human deaths per year are associated with it. Certain OP compound degrading bacterial enzymes have been isolated from soil and used as the therapeutic protection against OP compounds. Hence, manipulating culture independent approaches and metagenomics aids in personalized medicine and targeted therapeutic strategies. It plays a critical role in revolution of pharmaceutical industries (Pettit, 2004).

5. FUTURE RESEARCH DIRECTIONS

Recent advancements in soil metagenomics discloses the possible activities and behavior of uncultured microbes. For further improvements in future research there is a great need of understanding microbe-soil interactions. There is a need of engineering of soil microbes for establishment of improved soil and plants health. Probiotic *E. coli* is considered as example constructed by bioengineering to detect and sense pathogenic *P. aeruginosa* and precisely kill it (Foo *et al.*, 2017). Several microbes are involved in the synthesis of anti-cancer agents, immunosuppressants and anti-microbial agents. By manipulating these novel microbes by bioengineering we can make different low cost, effective therapeutic drugs which will aid in future clinical applications. Organic farming promotes biological cycles, NEU, soil biological activities and agricultural productivity as compared to using pesticides and herbicides which have many side effects. Moreover, soil also contains many virus particles. It is important to explore phage mechanisms and microbe infectivity, which can be done by viral metagenomics.

6. CONCLUSION

Soil microorganisms not only play a vital role in the environment but also biotechnologically. Most of these microorganisms cannot be cultured in labs. Though metagenomics and other techniques have helped us study the uncultured microbes, however, strategies to culture these unculturable microbes in labs should be devised. In this way, full potential of such microbes could be utilized.



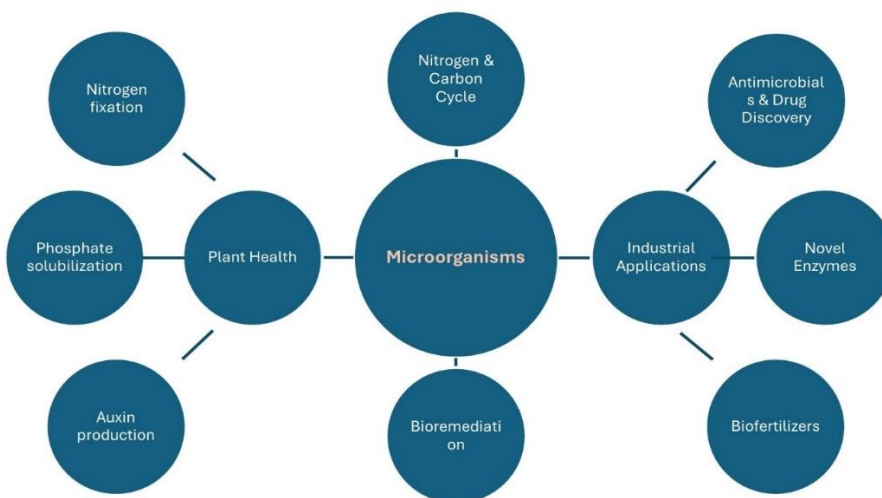


Figure 1. Some of the important roles and applications of soil microorganisms.

Conflict of Interest

The authors declare no conflict of interest.

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