



## Plant-microbe community dynamics in rhizosphere: Reviewing the grassroots ecology towards sustainable agriculture

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### ABSTRACT

The interaction between microbes and plants in rhizospheric environment is evident regarding sustainable development in agriculture. Microbes are involved in various metabolic activities in plant systems, which in turn help in plant health improvement. Eventually, plant-microbe interactions are connected with biogeochemical cycles. In this context, metagenomic study helps us to survey the microbial diversity in their natural niches, especially in rhizospheric regions. Noticeably, a diverse group of bacteria, fungi, and archaea are likely to be involved in plant growth promoting (PGP) activities. Variation in microbial communities in the rhizosphere depends on various parameters, such as soil organic matter, plant genotype, plant exudates, crop rotation, soil pH, nutrient cycling, etc. Some abiotic factors and chemical fertilizers have negative impact on crop productivity, influencing sustainable development of environment. Despite having negative impacts from climate change, microbes cope with this altered scenario and try to adjust themselves successfully and consequently promote plant growth by nutrient acquisition and stress tolerance approaches. Therefore, climate change has appeared as a big threat to the agricultural sector in recent past and this might be persistent in near future. However, the conservation of microbial diversity in the rhizospheric regions appears as one of the most promising options for long-term environmental sustainability.

**Keywords:** Agriculture, Climate change, Crop productivity, Sustainability

Agriculture means the continuous production of food and other essential commodities for human existence. Almost all countries in the world more or less depend on agriculture for their economy. Recently, agricultural sectors are facing the negative impacts of both the resources limitation, viz. soil fertility and water quality and drastic climate changes, i.e. extreme weather events (viz. drought, floods, and temperature fluctuation). Nitrous oxide (N<sub>2</sub>O), a greenhouse gas is produced during the usage of nitrogen fertilizer and in 2013, agriculture was responsible for 74% of N<sub>2</sub>O emissions in the United States (Rai *et al.* 2020). As a result, in order to meet the needs of people, we need sustainable agricultural systems (Biswas *et al.* 2018). Sustainable development may be defined as the management and conservation of natural resources (plant and animal production) to preserve ecological assets for future without compromising the present (Velten *et al.* 2015, Biswas *et al.* 2018). The major challenges to maintain sustainability include loss of microflora and microfauna, loss

of biodiversity, outdated production and yield strategies, lack of employment, regional imbalance in the economy, pollution, and global warming (Banerjee and Bandopadhyay 2018, Gupta *et al.* 2018). Besides these, physical factors like soil erosion, salinization, loss of soil organic matters (SOM), etc. are also some challenges that we have to cope with for crop improvement (Banerjee *et al.* 2019).

Soil can maintain its own health with the help of microbes, which are sensitive to land management and climate changes (Sabale *et al.* 2019). Soil-microbes complex interactions maintain soil fertility with the help of microbial metabolic by-products or by decomposition of SOM, nutrient cycling, stress management, and formation of soil aggregates in the rhizosphere (Basu *et al.* 2021). Rhizospheric microbial colonization is influenced by plant root exudates in the root-soil interface and it is the hotspot of microbial activities (Helming *et al.* 2018).

Conservation agriculture (CA) is an eco-friendly method for reducing soil disturbance by crop rotation, avoiding paddy straw burning on the field, input cost reduction, and crop yield enhancement by using biofertilizers (Chabert and Sarthou 2020). Four major bacterial phyla (Proteobacteria, Actinobacteria, Firmicutes, and Bacteroidetes) were identified from the soil (Bulgarelli *et al.* 2012). Exploration

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of all microbial niches in the rhizosphere is quite difficult but necessary as they are mostly unculturable (Khan *et al.* 2022). In this context, metagenomics study helps us to overcome major difficulties, advancing agricultural knowledge through the study of unculturable microbial genetic diversity study, complex environmental interactions, metabolic diversity, fates of soil carbon, etc. Various studies suggest that soil resources and microbial communities are under severe threats due to anthropogenic activities and climate changes. Actually, traditional uniform field management can cause yield losses due to receiving imbalanced distribution of nutrients, leading to resource wasting, soil degradation, environmental pollution, etc. For the development of a sustainable agriculture system, crops must get higher nutritional value as well as biotic and abiotic stress tolerance potentiality. Plant growth-promoting rhizobacteria/microorganisms (PGPR/PGPM) reduce the dependency on synthetic fertilizer, thereby enhancing soil fertility and crop productivity. This review primarily focuses on the factors influencing the richness of rhizospheric microbial communities and then explores the function of the microbial community controlling soil health (Khan *et al.* 2022).

#### Role of metagenomics in sustainable agriculture

Metagenomics is used to predict the dynamics and functional activities of microbial communities (Table 1),

allowing scientists to explore and answer fundamental scientific questions about relevancy of agriculturally associated microbial diversity (Goel *et al.* 2017). Through various metagenomics approach, we can monitor plant and animal health, crop production, yield improvement, pathogen and disease control, symbiotic association, resistance varieties, and novel molecules discovery. To maintain agricultural ecosystem biology, metagenomics assists for addressing different biotic and abiotic components associated with agriculture. Advanced sequencing and metagenomic analyses lead to the discovery of different beneficial microbes, which can be applied as biopesticides and biofertilizers. The biogeochemical cycles that sustain life on earth are largely mediated by soil microbiomes. They also play a role in metal transformation like iron, mercury etc (Iquebal *et al.* 2022). Huge loss in agricultural crops takes place due to easy adaptable antimicrobial resistant plant pathogens. The monitoring and early detection of plant pathogens from various habitats has been successfully done using metagenomics. Metagenomic studies on gut microbiota of different herbivores and rodents identified many plant viruses (Roossinck *et al.* 2015). Beneficial soil microbes improve plant health and growth through nutrient and vitamin supply, enhance developmental process and protect host from virulence factors. Various data from metagenomics is likely to understand the microflora, which are highly influenced by abiotic variables, associated with

Table 1 Role of different metagenomic techniques to detect microbial diversity

Method	Function	References
Phospholipids fatty acid analysis (PLFA)	a) Reveals that soil receiving synthetic fertilizer differ in bacterial composition that organically managed soil b) In heavy metal polluted areas community responses can be detected	(Chodak <i>et al.</i> 2013, Docherty <i>et al.</i> 2015)
Fatty acid methyl ester (FAME)	a) Provides information about the composition of microbial community based on grouping of fatty acids	(Sabale <i>et al.</i> 2019, Tanveer <i>et al.</i> 2016)
DNA re-association (G+C) content of DNA	a) Measures genetic complexity of microbial community and give estimation of microbial diversity a) Detects the changes in the microbial community composition b) Analysis of rare members community	(Fakruddin and Mannan 2013, Sabale <i>et al.</i> 2019) (Fakruddin and Mannan 2013)
Random amplified polymorphic DNA	a) Gives an idea about genomic variations between bacterial species b) Studies microbial diversity of industrially polluted soil	(Tilwari <i>et al.</i> 2013, Sabale <i>et al.</i> 2019)
Restriction fragment length polymorphism (RFLP)	a) Studies changes in bacterial community structure b) Distinguishes phylogenetically distant species or genera from environmental samples.	(Sano <i>et al.</i> 2021, Gupta <i>et al.</i> 2022)
Terminal restriction fragment length polymorphism (T-RFLP)	a) Measures the species richness and evenness as well as similarities between the samples	(Fakruddin and Mannan 2013, Finore <i>et al.</i> 2023)
Ribosomal intergenic spacer analysis (RISA)	a) Asses microbial diversity in a range of environmental niche	(Singh and Ambawat 2020)
Temperature/ denaturing gradient gel electrophoresis (TGGE/ DGGE)	a) Identifies the sequence variation in a number of genes from several different organism	(Sharma <i>et al.</i> 2020, Gupta <i>et al.</i> 2022)
DNA microarrays	a) Helps to detect and identify microbial diversity	(Fakruddin and Mannan 2013, Gunjal <i>et al.</i> 2023)

sustainable development in agriculture. Numerous functional assays based on metagenomic data, such as the antibiogram test and the colorimetric indole acetic acid assay, have been adopted to investigate diverse range of plant growth stimulating bacteria. They reveal about how the interactions among plant, microbiome, and environment are linked and furthermore, a little change in one variable might have an impact on others (Busby *et al.* 2017). Metagenomics is perhaps the solution of primary problems in agriculture (viz. environmental threats, economic threats, global warming, pollution, and urbanization) in order to increase food production and reduction of malnutrition (Dutta *et al.* 2020, Iquebal *et al.* 2022).

#### *Variation of rhizospheric microbial communities*

Bacterial, fungal and archaeal communities around the rhizospheric soil are more diverse than the bulk soil due to the rhizodeposition (exudation of plant-derived carbohydrates). Rhizodeposition and shedding stimulate microbial growth and multiplication and this phenomenon is known as rhizospheric effect (Wu *et al.* 2017). Microbial communities inhabiting or associated with the host plant may have positive or negative impacts on plants, e.g. sometimes, microbes compete with host plants for nutrients and water or show pathogenicity (Mendes *et al.* 2013). Different metagenomics and culturable techniques revealed microbial diversity in the vicinity of roots, and there is a proportional relationship between microbial diversity and resource heterogeneity.

#### *Bacterial community*

Bacterial communities in the rhizosphere are predominated by Proteobacteria, Acidobacteria, Actinobacteria, Verrucomicrobia, Bacteroidetes, Planctomycetes, Gemmatimonadetes, Firmicutes, and Chloroflexi (Lagos *et al.* 2015). These groups of bacteria have the ability to degrade lignin and cellulose by specific enzymes and considered as best colonizers of rice environments (Lagos *et al.* 2015). Some dominant species in the rhizosphere are *Rhizobium*, *Azospirillum*, *Burkholderia*, *Pseudomonas*, *Enterobacter*, etc. Alpha- and beta-proteobacteria are involved in the regulation of the carbon, nitrogen, iron, and sulfur cycles, production of phytohormones, nutrient uptake, PGP activities, antibiotics production, etc (Sun *et al.* 2015).

Gamma proteobacteria use a wide variety of plant exudates like fatty acids, amino acids, and sugars for efficient root colonization (Rashid *et al.* 2019). The metagenomics approach also identified Fusobacteria, Cyanobacteria, Bacteroidetes, Sphingobacteria, Flavobacteria, Deinococcus, Verrucomicrobia and Planctomycetes, colonizing rhizospheric regions of soil (Lagos *et al.* 2015). The presence of both anaerobic (e.g. *Clostridium*) and aerobic (members of Burkholderiaceae, Comamonadaceae, and Pseudomonadaceae) degraders in the rhizosphere strongly suggests that degradation processes at root environment are highly heterogenous (Lu *et al.* 2006). Iron reducers

(*Anaeromyxobacter* spp. and *Geobacter* spp.) inhabiting the rice rhizosphere are responsible for maintaining environmental carbon and iron dynamics (Lu *et al.* 2006). Endospore producing bacteria, *Bacillus* and *Clostridium* have a great impact on rhizospheric interactions, while the former one is related with the digestion of a wide variety of carbon sources.

#### *Archaeal community*

Archaea are essential for methanogenesis, ammonia oxidation, denitrification, hydrocarbon degradation, sulfate reduction, and tolerance of environmental hazards (Ding *et al.* 2019). Archaeal diversity is more prominent in aquatic plants rather than in terrestrial ones. It was also proven that, the network of archaeal community in rhizosphere is less complex than bulk soil (Zhang *et al.* 2020). Different groups of archaeal phyla, like Crenarchaeota, Thaumarchaeota, Euryarchaeota, Methanobacteriales, Methanomicrobiales, Methanosarcinales, Halobacteria, Methanospirillum, Methanomethylivorans, Methanosaeta, Nitrosopumilus, Nitrososphaera, etc. are found in the rhizosphere of rice and others crop plants (Liu *et al.* 2016). Methanogens are predominated in the rice rhizosphere (Lee *et al.* 2014). In order to increase metal and sulfur release rates into the environment, both autotrophic and heterotrophic archaeal members help to accelerate iron and sulfur oxidation (Buragohain *et al.* 2018). Some of the efficient phosphorus solubilizing archaea produce gluconic acid, fumaric acid, and tartaric acid to mobilize soil phosphorus (Rashid *et al.* 2019).

#### *Fungal community*

Rhizospheric fungal communities have sufficient ability to promote plant development and improve the quality of economically important plants. Fungi are directly linked to nutrient cycling and biocontrol activities. Fungal mycelia serves as important agent for carbon exchange between plant and soil microbes. Three major fungal phyla abundant in the rice rhizosphere are Ascomycota, Basidiomycota and Zygomycota (Qiao *et al.* 2019). Members of Chytridiomycota dominate on soybean, populus, and rice fields (Ding *et al.* 2019). *Aspergillus* spp. promote phosphorus solubilization while arbuscular mycorrhizal (AM) fungi uptake or transport phosphorus (Mendes *et al.* 2013) towards plant roots. Members of *Rhizophlyctis* and *Cladochytrium* have a particular role in carbon biogeochemical cycles by the decomposition of carbohydrates and cellulose (Eichorst and Kuske 2012). Mycorrhizal root and mycelium indirectly help in the growth and development of plants by providing niches for beneficial bacterial communities.

#### *Factors affecting the rhizospheric microbial community*

Different biotic and abiotic factors (viz. soil depth, SOM, porosity, pH, root exudation patterns, bioactive phytochemicals, O<sub>2</sub>/CO<sub>2</sub> concentration) interact with each other dynamically to stabilize and influence the agroecosystems with profound effects on plant physiology

and development (Lundberg *et al.* 2012, Ding *et al.* 2019). For example, root development in *Arabidopsis* is controlled by complex bacteria-bacteria interactions (Finkel *et al.* 2020). Higher air and soil temperatures, moisture, and greater precipitations increase microbial growth and activity. Drought alters soil properties and as a result, oligotrophic phyla, sporulation, biosynthesis and functions of antibiotics, and osmolytes of microbes change dramatically (Naylor and Coleman-Derr 2018). The microbial load in the soil affects soil porosity, aeration, nutrient cycling, and water-holding capacity. Plant genotype, crop rotation, cultivation period (accumulation of organic carbon), and soil pH (pH decreases as depth increases) are the regulatory factors that alter bacterial and fungal composition in rhizosphere (Naylor and Coleman-Derr 2018). SOM is the main edaphic factor that determines local scale of bacterial diversity, whereas climate and soil pH are regulatory factors for regional and continental scales. The phylogenetic diversity of bacteria increases in temperate forests as compared to subtropical or tropical forests (Tian *et al.* 2018). Soil heterogeneity is the driving force for bacterial community diversity. Whereas, geographic distance and fungal communities are more sensitive to soil depth unlike bacterial community (Liu *et al.* 2016). Rhizomicrobiomes are also influenced by plant domestication (which sometimes enhances fungal

alpha diversity) (Chang *et al.* 2021). Archaeal diversity is accelerated by the presence of bacterial and fungal species and reduced by increasing soil salinity and nitrogen loss (Zhang *et al.* 2020).

Strigolactone secreted from roots induces the branching of AM hyphae, whereas jasmonic acid signaling reduces root endophytic communities (Liu *et al.* 2017). If the temperature rises to 5°C, the bacterial-to-fungal ratio is also increased, indicating that the fungal community adapted themselves to lower temperature than bacteria (Dubey *et al.* 2019). Denitrifying bacterial orders (e.g. Burkholderiales, Rhodocyclales, and Rhizobiales) respond greatly on the basis of environmental changes in the paddy field (Yoshida *et al.* 2009). Fluorescence *in situ* Hybridization (FISH) study detected that the addition of nitrate largely increased the growth of denitrifying bacteria like *Bacillus*, *Dechloromonas* and addition of sulfate stimulated the growth of *Desulfosporosinus* and *Geobacter* (Scheid *et al.* 2004).

*Plant exudates influence microbial communities*

Various plant species have different effects on rhizospheric soil microbial biomass and activity (de Sousa *et al.* 2019). Plant roots exudate variety of sugars like glucose, fructose, and sucrose depending on their developmental stage, and their genetic makeup (Lundberg *et al.* 2012).

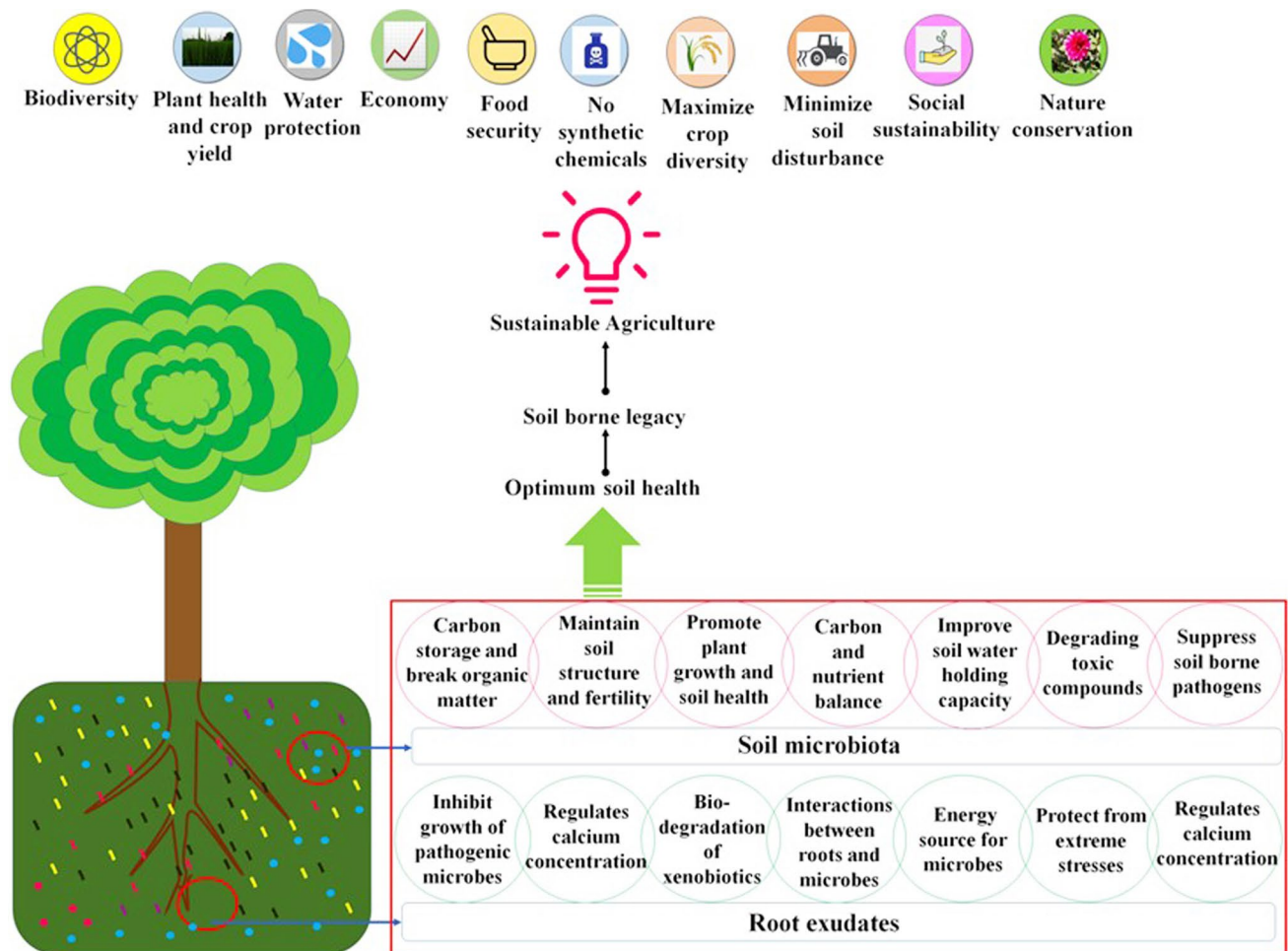


Fig 1 Role of root exudates and soil microbiota to maintain sustainable agriculture.

These exudates function as messengers that stimulate interactions between roots and soil microbes, which attract both beneficial and detrimental organisms (Table 2). Root associated microbes sense these metabolites with the help of chemotaxis or dedicated receptors and promote biofilm formation (Liu *et al.* 2016, O'Banion *et al.* 2020). Phenolic compounds (coumarins and flavonoids) are secreted by the plant under iron and phosphate limiting conditions also sensed by microbes to help in nutrient mobilization, *nod* gene expression and destroy pathogenic bacteria. Root exudates and soil microbial communities are pre-requisites to maintain soil health which is one of the main parameters of sustainable agriculture (Fig 1).

#### Importance of plant microbes in nutrient acquisition

Rhizospheric microbes (bacteria, cyanobacteria, fungi, etc.) are involved in PGP by nutrient mobilization as macro (C, H, O, etc.) and micronutrients (Mn, B, Co, Mo, Zn, Si, etc.) are required in optimum concentration for plant growth (Fig 2) (Kabiraj *et al.* 2020). Plant-microbes symbiotic associations are largely determined by cost-benefit ratios, where microbes help in nutrient acquisition.

Ideally, agriculturally important crops show major

association with the AM (Arbuscular mycorrhizae) fungi and members of Glomeromycota that induce systemic resistance, hormone production, uptake of P, Fe, Zn, etc. and increase root biomass (Prakash *et al.* 2015). AM fungi enable the mobilization of less soluble compounds to plants by their alkaline and acid phosphatase activity (Naik *et al.* 2019). AM fungi make symbiotic association with plants and supply 90–100% of the plant phosphorus demand and in return, fungi takes up carbon from plants in the form of hexose, sucrose, and fructose. The intracellular mycelia of fungi interact with the apoplastic region of the plant and transfer nutrients to the plant cells via specific transporters. However, the detailed mechanism of this transportation remains unclear. AM fungi increases root surface area and the narrow diameter of fungal hyphae allow them to contact small pores that help to absorb nutrients from the soil, and for this reason, AM-associated plants show an increase in shoot biomass production as compared to non-AM plants (Ganugi *et al.* 2019). Both C<sub>3</sub> and C<sub>4</sub> plant species can be benefited from AM fungi but C<sub>3</sub> plants are less responsive to AM fungi than C<sub>4</sub> (Frew 2019). A study showed that treatment of biochar (a carbon compound) with AM fungi increased the nutrient uptake (particularly N, P, K, S, Zn)

Table 2 List of different root exudates found in the rhizosphere

Types of root exudate	Example	Function	Reference
Amino acids and amides	All 20 proteinogenic amino acids, homoserine, aminobutyric acid, mugineic acid	Inhibits nematodes	(Neumann and Romheld 2000)
Aliphatic acids	Formic, acetic, butyric, popionic, malic, citric, isocitric, oxalic, fumaric, malonic, succinic, maleic, tartaric, oxaloacetic, pyruvic, oxoglutaric	Regulates calcium concentration	(Sasse <i>et al.</i> 2018)
Aromatic acids	p-Hydroxybenzoic, caffeic, p-coumaric, ferulic, gallic, genistic, salicylic, synaptic, syringic	Stimulate biodegradation of xenobiotics.	(Hayat <i>et al.</i> 2017)
Organic acids	Ascorbic, benzoic, acetic, aconitic, citric, lactic, malic, tetric, tartaric, glycolic	Utilize microbes as energy source	(van Dam and Bouwmeester 2016)
Enzymes	Amylase, protease, peroxidase, invertase, phosphatase, polygalacturonase	Inhibits growth of pathogenic microbes	(van Dam and Bouwmeester 2016)
Fatty acids	Linoleic, linolenic, oleic, palmitic, stearic acids	Provide energy for various metabolic activities in plant	(Sasse <i>et al.</i> 2018)
Sugars and polysaccharides	Sucrose, glucose, fructose, maltose, mannose, arabinose, raffinose, xylose	Enhance the growth of microbes, provide plant structural component	(Hayat <i>et al.</i> 2017)
Sterols	Stigmasterol, cholesterol, campesterol, sitosterol	Regulates plant growth (PG)	(Neumann and Romheld 2000)
Nucleotides	Adenine, guanine, uridine or cytidine	Stimulate interactions between roots and microbes	(Neumann and Romheld 2000)
Allomones	Jugulone, sorgoleone, DIMBOA, DIBOA	Act as defense molecules	(Neumann and Romheld 2000)
Indole compounds	Indole-3-acetic acid, brassitin, sinalexin, brassilexin, camalexin glucoside.	Promote plant growth	(Hayat <i>et al.</i> 2017)
Flavonols	Naringenin, quercetin, naringin, rutin, genistein, strigolactone	Protect plant from biotic and abiotic stresses and acts as UV filter	(Hayat <i>et al.</i> 2017)
Glucosinolates	Cyclobrassinone, desuphoguconapin, desulphoprogoitrin	Acts toxic to soil borne pathogens	(Sasse <i>et al.</i> 2018)
Anthocyanins	Cyanidin, delphinidin, pelargonidin	Protect plant against extreme temperature	(Sasse <i>et al.</i> 2018)

of wheat (Ganugi *et al.* 2019).

*Soil microbes improving plant health under changing climate*

Microbes are important components in maintaining soil health, acting as a safeguard for sustainable development by sustaining their cellular homeostasis in extreme environments and promote the growth of host plant as well as crop yield (Laha *et al.* 2020, Chang *et al.* 2021). Usually, soil microbes facilitate plants to uptake different nutrients like N, P, K, Fe, Zn, etc through fixation, solubilization, and mobilization (Yadav *et al.* 2017). Archaea and bacteria may be involved in nitrogen fixation, phosphorus solubilization, siderophore production, IAA, GAs, cytokinins production, ammonia

oxidation, etc. (Yadav *et al.* 2017). However, PGPR degrade ethylene precursor, 1-aminocyclopropane-1-carboxylate (ACC) by ACC deaminase to form a healthy root system (Rai *et al.* 2020). Microbial siderophores can chelate ferric ions from the soil and transfer them to plants whenever it is required. Volatile organic compounds (VOCs) produced by PGPR have a role in PG, stress tolerance, and induced systemic resistance (ISR) against pathogens (Rai *et al.* 2020). Some rhizospheric microbes secrete hydrolytic enzymes or certain metabolites that inhibit fungal pathogens (Saxena *et al.* 2014). Arbuscular mycorrhizal fungi (AMF) increases mineral nutrient absorption through the establishment of mutualistic interactions with their host plants (Bouskout *et al.* 2022, Dounas *et al.* 2022). Soil microbes (bacteria and

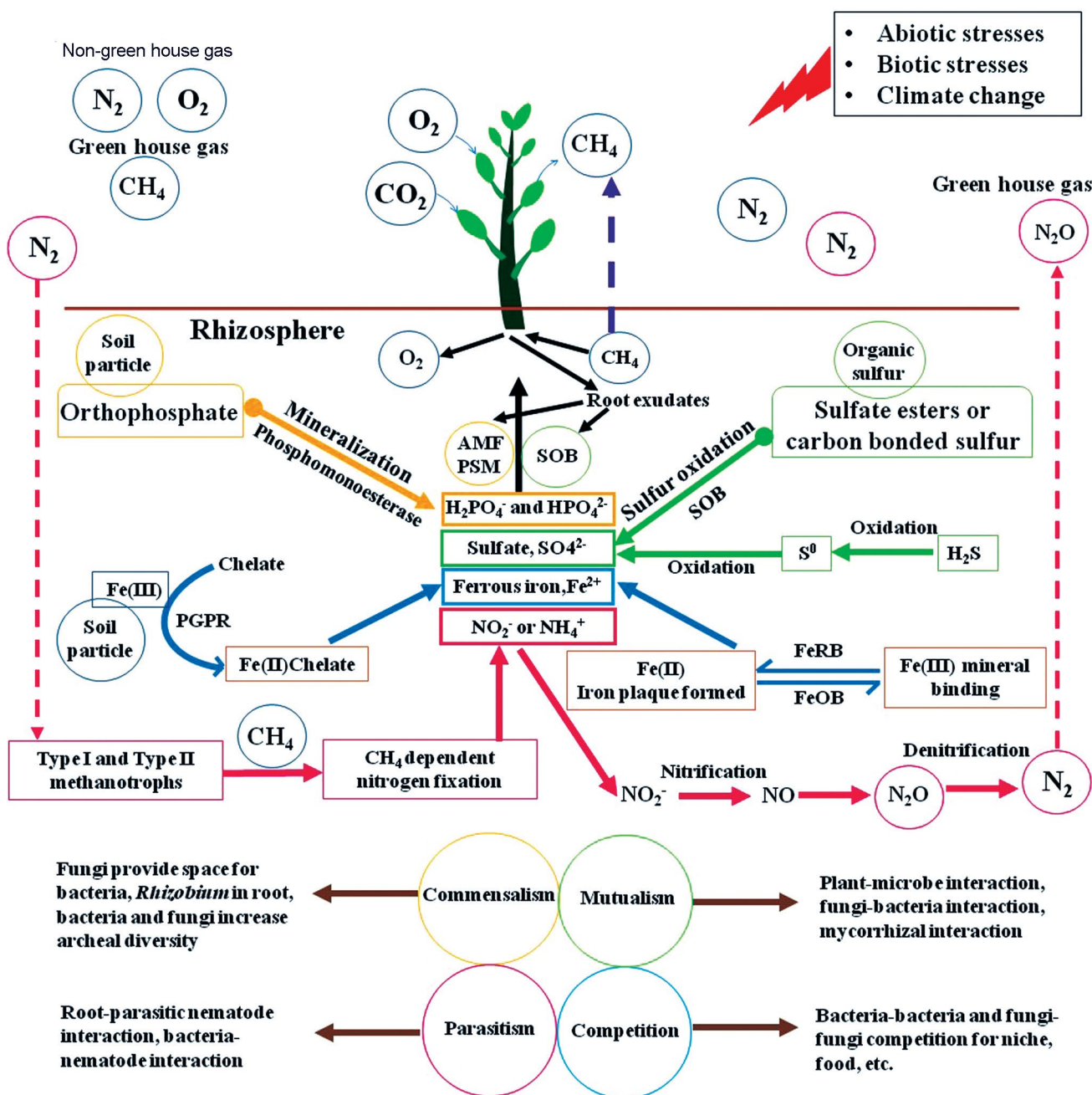


Fig 2 Role of microbes in nutrient acquisition and interactions in the rhizosphere.



fungi) can dissolve silicon from a variety of basic minerals and the dissolved form is taken up by plants to enhance crop productivity by providing resilience to numerous biotic (insects and pathogens) and abiotic (salt stress, nutritional toxicity, heavy metal toxicity etc.) stresses (Chakraborty *et al.* 2021, Dutta and Bandopadhyay 2022). It is predicted that silicate solubilizing bacteria (SSB) produce IAA and other organic acids to dissolve silicate (Raturi *et al.* 2021). Crenarchaeota (archaea) act as soil nitrifiers and are an important member of soil denitrification processes (Treich *et al.* 2005). Under stringent environmental conditions, archaea can degrade glycogen and are able to fix CO<sub>2</sub>, which in turn serves as an energy source for other organisms and improves growth-promoting properties (Taffner *et al.* 2019). Both bacteria and archaea produce a universal stress protein (USP) that helps host plants thrive in abiotic stress conditions (Alori *et al.* 2020).

#### *Microbes in controlling biogeochemical cycles*

Abiotic and biotic factors dependent biogeochemical cycles (BC) are the foundations of environmental sustainability. Generally, the rhizospheric soil (where carbon compounds are excreted from roots) is one of the most active ecosystems for nutrient cycling. Thus, a considerable amount of photosynthetic carbon is deposited underground and eventually converted to SOM by rhizodeposition. SOM breakdown rate is driven by indigenous microbial metabolism and environmental variables like temperature, pH, soil water capacity, etc. In addition, manure application can also change the structure and diversity of the iron (Fe)-plaque forming microbial communities as well as sulphur, iron, and arsenic cycles regulating microbial communities, such as *Bradyrhizobium*, *Burkholderia* and *Ralstonia* (Tang *et al.* 2021).

CH<sub>4</sub> dependent nitrogen fixation is performed by both type I and type II methanotrophs and after fixation, it is used by the plant with high efficiency (Wei *et al.* 2019). During the midseason drainage in the paddy fields, reduced forms of sulfate and Fe(III) promote the growth of sulfate and iron reducing microbes respectively and these microbes outcompete the methanogens and restrict their growth (Ding *et al.* 2019). This mechanism provides the economic benefits of rice yields and water-saving properties.

The dead organic microbial mass (e.g. cell wall fragments, exoenzymes, osmolytes, etc.) is the primary constituent of SOM (Wei *et al.* 2019). The abundance of carbon-fixing bacteria decreases with soil depth, and CO<sub>2</sub> fixing capability of soil is verily influenced by bacterial community composition along with the presence of autotrophic microorganisms. It was speculated that archaea also participate in the carbon cycle (Yadav *et al.* 2017).

Most orthophosphates are firmly bonded to soil particles (in insoluble, immobilized, precipitated form), so only a small quantity of soil phosphorus is accessible (1–5%) for plants, as plants can only uptake soluble monobasic (H<sub>2</sub>PO<sub>4</sub><sup>-</sup>) and dibasic (HPO<sub>4</sub><sup>2-</sup>) ions of phosphate (Fig 2). AM fungi and Phosphate solubilizing microbes (PSM),

including *Burkholderia*, *Bacillus*, *Sphingomonas*, etc are present in rice fields, showing increased crop yield by solubilizing more available phosphorus to plants (Wei *et al.* 2019). Different organic acids are produced by the PSMs and consequently, soil pH is decreased. This step increases phosphorus availability to plants. Apart from that, other factors like air temperature and soil phosphorus availability are the determinant factors for the activity of PSMs (Ho *et al.* 2017). Plants primarily uptake inorganic sulfate (SO<sub>4</sub><sup>2-</sup>), but in the agricultural fields, most of the soil sulfur (>95%) is present as sulfate esters or as carbon bonded sulfur (sulphonates or amino acid sulfur) rather than inorganic sulfate (Kertes and Mirleau 2004). Sulfur oxidizing bacteria (SOB) like *Thiobacilli* carry out sulfur oxidizing processes, making their byproduct available to plants (Rana *et al.* 2020).

Plants utilize ferrous forms of iron (Fe) rather than ferric. The ferric form of Fe is reduced by rhizospheric Fe(III)-reducing bacteria (FeRB). Fe(II)-oxidizing bacteria (FeOB) further oxidize ferrous ions to ferric ones. By these two distinct mechanisms, the iron cycle is completed (Wei *et al.* 2019). Fe oxidation is triggered by the radial loss of O<sub>2</sub> in high temperatures. So, in summer, oxidation of Fe(II) is predominated and reduction of Fe(III) is a continuous process throughout the year.

Nitrogen is a critical limiting element for PG and crop productivity. It is taken up by plant roots mainly as nitrate (NO<sub>3</sub><sup>-</sup>), sometimes as nitrite (NO<sub>2</sub><sup>-</sup>), or ammonium (NH<sub>4</sub><sup>+</sup>) form. Nitrogen fixation, dissimilatory nitrate reduction to ammonia (DNRA), nitrification, ammonification, and denitrification are the metabolic processes of nitrogen cycle (Rashid *et al.* 2019). Nitrogen is fixed as ammonia, nitrate, or nitrite while fixed nitrogen oxides (NO<sub>3</sub><sup>-</sup> and NO<sub>2</sub><sup>-</sup>) are reduced to gaseous end products like nitric oxide (NO), nitrous oxide (N<sub>2</sub>O) (greenhouse gas) and nitrogen gas (N<sub>2</sub>) by many types of bacteria and archaea. Through this procedure, nitrogen cycle is completed, resulting in nitrogen loss from the agricultural fields through denitrification.

Microbes can play direct (by biotransformation) or indirect roles in mobilizing or immobilizing arsenic (As) in the soil-rice ecosystem and accumulation of arsenic in rice grains. Arsenite [As(III)], arsenate [As(V)], monomethylarsonic acid (MMA), and dimethylarsinic acid (DMA) are the four types of As typically accumulated in rice grains (Fig 3) (Jia *et al.* 2013, Let *et al.* 2022). Dimethylarsinous acid (DMA) is uptaken by rice plant roots and transported into grains (Kuramata *et al.* 2015). The mobilization of As is increased when arsenate is reduced to arsenite. In the rhizospheric soil, manure enhances the relative abundance of *Rhizobium*, *Burkholderia*, *Sphingobium* and *Sphingomonas*, which sometimes harbors arsenate reductase genes (*arsC*) (Kabiraj *et al.* 2022). A notable benefit provided by PGPMs is altered speciation of As in the soil by biomethylation that results in shifting of As in the rhizosphere (Upadhyay *et al.* 2018).

*Impacts of chemical fertilizers and biofertilizers on*

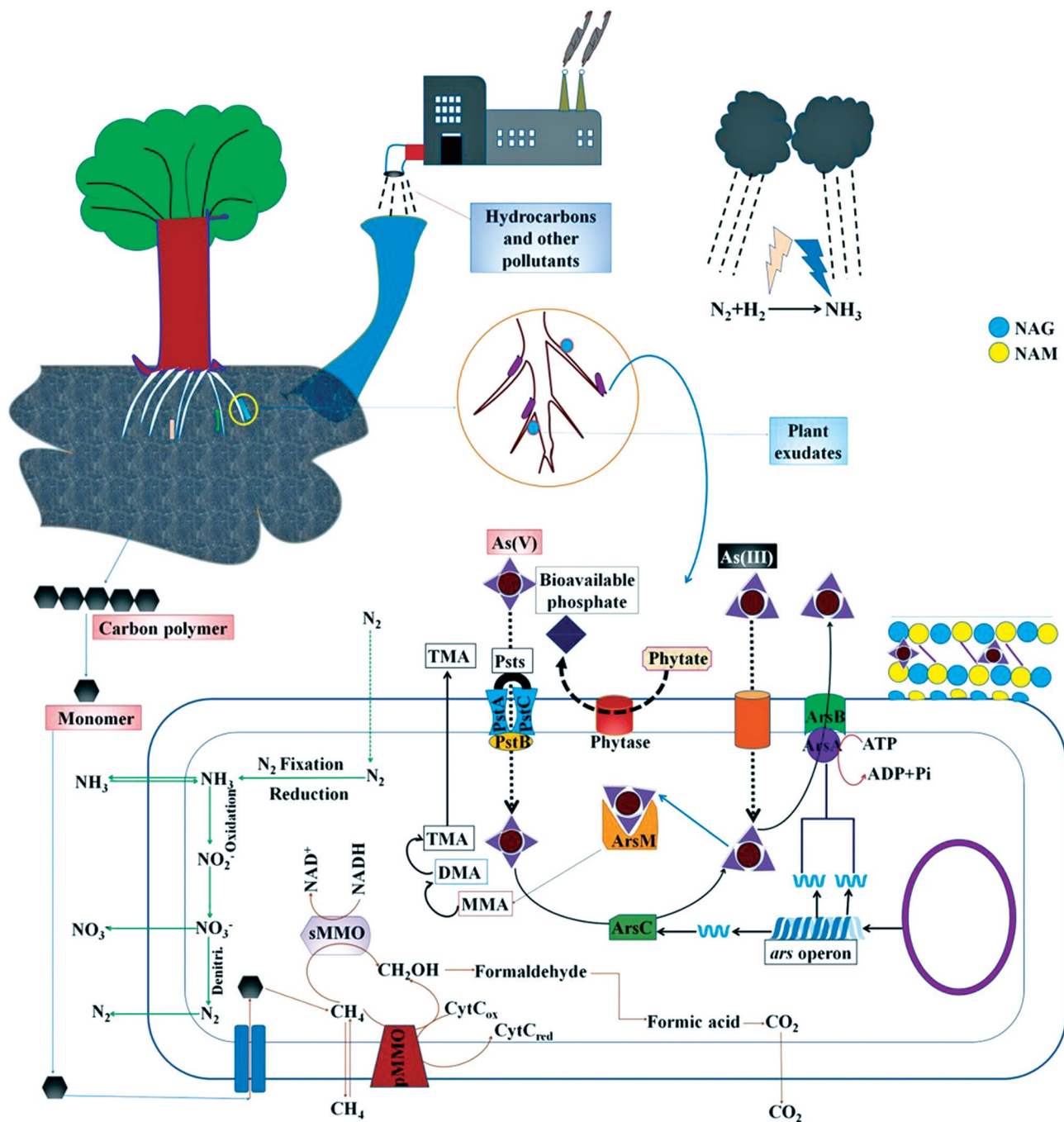


Fig 3 Microbes controlling biogeochemical cycles.

*different crops*

Higher dosage of chemical fertilizers leads to mineralization and SOM acidification, non-biodegradable harmful substances accumulation, water pollution, early decay of the harvested yam tubers, loss of flavor, taste, and aroma in crops, etc. The use of optimum nitrogen fertilizer, i.e. concentration gives maximum yields in plants, thereby resulting in no loss of microbial diversity and promoting extensive root system and broad canopy development (Singh 2018). However, higher concentration negatively interferes with microbial metabolism and soil-microbe symbiosis which alters carbon to nitrogen ratio in the field (Seneviratne

2009). In contrast, biofertilizers have long-lasting effects due to their slow nutrient release, and they promote plant growth by increasing the primary supply of nutrients, activation of plant disease resistance genes, mycorrhizal development, production of antibiotics and phytohormones, restoring soil nutrient cycle, etc. (Sneha *et al.* 2018). The association of PGPR with certain plants can help to combat certain abiotic stresses (cold, high temperature, salinity, heavy metals) and prevents plants from dying (Kabiraj *et al.* 2020). In order to colonize their hosts, asymptotically endophytes are involved in multipartite interactions and modulate plant growth and development (Bulgarelli *et al.* 2012, Schulz



*et al.* 2015). For example, inoculating tomato seeds with PGP psychrotolerant bacteria from the genera *Arthrobacter*, *Pedobacter*, *Flavimonas*, *Flavobacterium* and *Pseudomonas* considerably enhanced plant height, root length and repaired membrane damage. Higher amounts of glycine betaine-like compounds are produced by the bacterium, *Pseudomonas pseudoalcaligenes*, resulting in better salinity stress tolerance in rice. Vigna's phytoprotection against mercury (Hg) was aided by *Photobacterium halotolerans*, which increased productivity while lowering Hg translocation into the bean pods (Ho *et al.* 2017).

### Conclusion

The rhizosphere is considered one of the most valuable unexplored biomes of microbial communities. Microbial diversity in rhizosphere can be changed depending upon many factors like soil organic matter, soil pH, soil depth, CO<sub>2</sub> etc. So, it becomes necessary to explore such an important site of microbial communities, which are required to be conserved for sustainable agriculture. Plant growth promoting microbes act synergistically to improve nutrient acquisition under stresses and induce systemic resistance (ISR) within plants against pathogens. Biogeochemical cycle not only store elements and uses energy but also maintain proper microbial diversity to sustain soil health as well as crop yields. Still, it is quite difficult to predict what kind of multipartite interactions are ongoing in the rhizosphere. It appears that the presence of any keystone species may regulate all these crucial interactions. Hence, microbial biome in the rhizosphere is an indispensable resource of research that helps to explore this eerie world of microbes.

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