



# Delineation of mechanistic approaches of rhizosphere microorganisms facilitated plant health and resilience under challenging conditions

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## Abstract

Sustainable agriculture demands the balanced use of inorganic, organic, and microbial biofertilizers for enhanced plant productivity and soil fertility. Plant growth-enhancing rhizospheric bacteria can be an excellent biotechnological tool to augment plant productivity in different agricultural setups. We present an overview of microbial mechanisms which directly or indirectly contribute to plant growth, health, and development under highly variable environmental conditions. The rhizosphere microbiomes promote plant growth, suppress pathogens and nematodes, prime plants immunity, and alleviate abiotic stress. The prospective of beneficial rhizobacteria to facilitate plant growth is of primary importance, particularly under abiotic and biotic stresses. Such microbe can promote plant health, tolerate stress, even remediate soil pollutants, and suppress phytopathogens. Providing extra facts and a superior understanding of microbial traits underlying plant growth promotion can stir the development of microbial-based innovative solutions for the betterment of agriculture. Furthermore, the application of novel scientific approaches for facilitating the design of crop-specific microbial biofertilizers is discussed. In this context, we have highlighted the exercise of “multi-omics” methods for assessing the microbiome's impact on plant growth, health, and overall fitness via analyzing biochemical, physiological, and molecular facets. Furthermore, the role of clustered regularly interspaced short palindromic repeats (CRISPR) based genome alteration and nanotechnology for improving the agronomic performance and rhizosphere microbiome is also briefed. In a nutshell, the paper summarizes the recent vital molecular processes that underlie the different beneficial plant–microbe interactions imperative for enhancing plant fitness and resilience under-challenged agriculture.

**Keywords** Rhizosphere microbiome · Nutrient acquisition · Phytohormonal modulation · Quorum quenching · Innate immunity · Genome editing

## Introduction

Various abiotic (drought, cold, salinity, alkalinity, floods, and mineral imbalance) and biotic stresses (imposed by pathogenic fungi, bacteria, and nematodes) adversely

affects plant growth, development, and yield. In addition to agronomic and plant breeding approaches, plant growth-promoting microbes are also gaining attention for improving crop productivity under abiotic and biotic stresses. The use of plant-growth promoting microbes has been promoted as

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one of the main strategies to alleviate such stresses as they can modulate host physiological and molecular responses to alleviate stress-induced cellular injuries. Plant micro-environments, chiefly the rhizosphere and rhizoplane, are abundantly occupied by diverse soil microbial communities with varying functional aspects. The rhizosphere, which is the narrow zone of soil surrounding plant roots, can consist of up to  $10^{11}$  microbial cells per gram of root and more than 30,000 prokaryotic species (Bhardwaj et al. 2014). The rhizosphere microbiome includes all those microbial members, which colonizes the rhizosphere and are involved in the symbiotic, neutral and pathogenic interactions with the host plants. Plant-rhizosphere microbiome (PRM) interaction in the rhizosphere is two-directional, in which microbes also acquire nutrients from the carbon-rich compounds released in the form of root secretions (Olanrewaju et al. 2019). The structural and functional abundance of rhizospheric microbes is mainly attributed to the root exudates accumulated as rhizodeposits (Zhalnina et al. 2018). Rhizodeposits include substances leached from sloughed-off root cells, mucilages, volatiles, soluble lysates, and exudates (Weston et al. 2015; Musilova et al. 2016). Different organic (such as polysaccharides, monosaccharides, organic acids, amino acids, phytohormones, and phenolics) and inorganic compounds (water, ions, electrons, and ubiquitous H<sup>+</sup>) are the major components of rhizodeposits (Gupta et al. 2020). The successful establishment, effective root colonization, and benefits to plants by the specific microbiota mainly depend on the rhizodeposits (Schmidt et al. 2014; Weston et al. 2015; Musilova et al. 2016). Moreover, the pattern of organic compound utilization, chemotaxis behavior, and synthesis of proteins and lipopolysaccharides (LPSs) determine the fate of rhizosphere competence by specific microbe (Lugtenberg and Kamilova 2009). Rhizodeposit influences overall rhizospheric processes and stimulate interactive metabolic cross-talk, linking different biosynthetic pathways and networks in the successful PRM interactions.

The rhizosphere colonizing plant growth-promoting rhizobacteria (PGPR) is a viable option for increasing performance and yield (Liu et al. 2020) under adverse environment. Upon rhizosphere colonization, PGPR triggers a broad array of biochemical, physiological, and molecular alterations in host plants via activating numerous metabolism and development-linked metabolic pathways (Bharti et al. 2016). PGPR support the growth and resilience of crops via the acquisition of plant nutrients, a transformation of the unavailable soil nutrients to plants accessible form, curtailing pathogens activities, priming plant immunity via eliciting host defense pathways, and mitigation of abiotic and biotic stresses (Meena et al. 2017a, b; Gouda et al. 2018). Under abiotic stresses, many benefits offered by the diverse PGPR can be utilized by understanding the biochemical, molecular, and physiological facets involved in their root zone

enrichment and favoring plant growth and fitness (Hassani et al. 2018). Henceforth, understanding the PRM interrelationships and factors helpful in recruiting the useful microbiome have been a foremost researchable area for the last several years (Compant et al. 2019). A better perceptive of the dynamic interactions of the plant-microbiome-environment axis will smooth the progress of the knowledge-guided, precision-delivery of the plant microbiome to stimulate plant growth and health under a specific set of environments. Using recent genetic studies, including “multi-omic” approaches (metagenomics, transcriptomics, metaproteomics, and metabolomics), high throughput sequencing (HTS), and next-generation sequencing (NGS), the functional and structural aspects of rhizosphere microorganisms have been elucidated (Meena et al. 2017a, b; Basu et al. 2018). Genome modification technologies like CRISPR/Cas9 have rapidly progressed and made it possible to acquire precise genetic information and decipher the molecular facet of PRM interactions (Knott and Doudna 2018). The CRISPR/Cas9 tool could further help augment details of microbiome-mediated improved crop productivity, disease tolerance, and resilience (Zaidi et al. 2019).

With this background, the present review aimed to decode the critical mechanisms of PGPR and other plant beneficial rhizosphere microbiome enhancing plant growth and health and gain precise information on how these microbiome impacts plant development via modulation of host plants biochemical, physiological, and molecular responses under suboptimal growth conditions. Furthermore, we have also narrated the possible use of modern scientific tools such as CRISPR/Cas9-mediated genome modification and nanotechnology to improve the performance of the crop and associated beneficial microbiome, respectively.

## Metabolites mediated signaling network and communication systems in the PRM interactions

### Rhizosphere microbiome mediated signaling communication with host plants

Different signaling molecules of microbial origin initiate rhizosphere microbe to plant interactions. Microbially produced peptidoglycan, chitin, flagellin, exopolysaccharides (EPS), hormones, volatile organic compounds (VOCs), antibiotics, and extracellular enzymes are signaling molecules. These molecules are vital in establishing microbial interplay with the host plants via activation of complex metabolic pathways and gene regulatory networks (Romera et al. 2019). Microbial signaling molecules have an explicit and preserved chemical structure/pattern, termed microbe-associated molecular patterns (MAMPs). The MAMPs are

recognized by plant pattern recognition receptors (PRRs). Subsequently, a host defense system gets elicited via phytohormonal (salicylic acid (SA), jasmonic acid (JA), and ethylene (ET)) based modulation of signaling cascade network (Offor et al. 2020; Sharifi and Ryu 2018; Romera et al. 2019). Among the MAMPs, flagellin, chitin, and EPS are the well-known signaling compounds ensuring their cross-talk with host plants (Jelenska et al. 2017; Lawrence et al. 2020; Kawaharada et al. 2015).

The EPS produced by PGPR aids in allowing mutualism between nitrogen-fixing rhizobia with its host, e.g., the symbiosis of *Mesorhizobium loti* strain R7A with *Lotus japonicus* initiates only after the firm binding of EPS with the host receptor (Kawaharada et al. 2015). Further, rhizobium unable to synthesize EPS cannot penetrate the root and form a nodule (Kawaharada et al. 2015). Accordingly, many strains of succinoglycan producing *Sinorhizobium meliloti* Rm1021 establish nodulation and symbiosis with alfalfa roots (Costa et al. 2018). Furthermore, the role of Nod and Myc factors (secreted by rhizobia and AM fungi, respectively) as signaling molecules in a symbiosis PRM interaction is well reported (Venturi and Keel 2016). Certain metabolites produced by PGPR are involved in interspecies communication and ascertaining the intraspecific interplay. For instance, bacterial and fungal VOCs may alter root metabolism, physiological and hormonal pathways, and biomass production in the host plants via direct and indirect ways (Schulz-Bohm et al. 2017). The biosynthesis of certain VOCs relies on the GacS/GacA two-component regulatory system, as recently demonstrated in a few rhizobacteria (Cheng et al. 2016; Ossowicki et al. 2017). Rhizosphere colonizing and VOC (2, 3-butanediol) secreting *Bacillus* strain noticeably improves growth and development and primes innate immunity against the pathogen in *Arabidopsis thaliana* (Venturi and Keel 2016). Furthermore, many pathogen biocidal antibiotic compounds (such as diacetyl phloroglucinol (DAPG), siderophore, cyanide, pyrroles, pyrrolnitrin, phenazines, quinolone and iturins, bacillomycin, fengycins, surfactins, and hydrolytic enzymes) indirectly promote plant growth via activation of phytohormonal based signaling pathways (Navarro et al. 2019). Upon sensing microbial signaling molecules, host plants depict several biochemical and physiological responses such as cell wall lignifications, deposition of suberin, and callose in tissue (Mhlongo et al. 2018). Likewise, microbially synthesized hormones may also function as plant signaling compounds. The findings of Salas-Marina et al. (2011) showed that root colonization of *A. thaliana* by *Trichoderma viride* starts with the exchange of indole acetic acid (IAA)-related indole involved in the activation of systemic resistance against phytopathogens. In brief, the findings of the above representative studies reveal the pivotal roles of various signaling metabolites in establishing intercommunication with the host plant.

Following recognition and establishing a relationship with the specific microbe, host plants exhibit enhanced growth, metabolism, and development along with innate immunity. Such gathered information is pivotal in harnessing the PRM interaction in a beneficial way for agriculture.

### Host plant mediated signaling interaction with rhizosphere microbes

The presence of vast microbial diversity in the rhizosphere indicates the potential role of phytosecretion in two-way PRM interactions. These phytochemicals selectively chemo-attract the specific microbial group in the rhizosphere. Till now, the role of very few plant secreted compounds in altering the structural assemblage and functional aspects of the rhizosphere microbiome have been reported. Perhaps, the best-elucidated signaling network in PRM interplay is in legumes with N-fixing rhizobia. In legumes-rhizobia symbiosis, legume roots release flavonoid compounds (2-phenyl-1,4-benzopyrone derivatives) that induce the transcription of rhizobial Nod factors genes. Nod genes encode lipochitooligosaccharides (LCOs), a chitin core made up of  $\beta$ 1, 4 linked polymer of N-acetylglucosamine (GlcNAc), also known as nodulation factors (Rosier et al. 2018). Bacterial LCOs are perceived by the LysM receptor (lysin motif-containing receptor-like kinase family) present in legume roots, which later stimulate a well-exemplified signal cascade involved in the root nodulation (Rosier et al. 2018). Similarly, an LCO-kind signaling compound (Myc-LCOs) has been recently demonstrated in arbuscular mycorrhizal fungi (AMF) too. Notably, some roots exudate molecules may function as sensing signals for AMF. For example, strigolactones (SLs), a carotenoid-derivative phytohormone in rhizodeposits facilitate host plants mutualism with rhizobia and AMF (López-Ráez et al. 2017). Further, SLs may also modify root architecture, especially during phosphorus deficiency, enhance lateral root branching, and improve nutrient accessibility (Andreo-Jimenez et al. 2015). More recently, the role of cutin monomeric units as a specific class of plant signaling molecule in their mutual interaction with AMF has been demonstrated. Two loci responsible for cutin monomer production, *RAM1*, which encodes a GRAS domain transcription factor, and *RAM2*, which encodes an acyltransferase (both required for root colonization by AMFi), have been identified in mutants *Medicago truncatula*-AMF symbiosis studies (Venturi and Keel 2016). Some crop-specific phytochemicals can also substantially help recruit specific microbial groups in their rhizosphere. This phenomenon has been observed in specific crop-rhizosphere microbe interactions.

For instance, citric acid and fumaric acid released from cucumber and banana roots explicitly attracted *Bacillus amyloliquefaciens* SQR9 and *B. subtilis* N11, respectively

(Zhang et al. 2014). The heteroaromatic secondary metabolite benzoxazinoids secreted by maize roots favorably recruits unique bacterial and fungal genera in the rhizosphere (Cotton et al. 2019). In response to specific root exudates such as arabinogalactan, PGPR indirectly benefits the host plant by controlling the root pathogens (Xie et al. 2012). Apart from these, distinct plant metabolites may also function precisely in the legume-rhizobia symbiosis (Abdel-Lateif et al. 2012), AMF network branching and its expansion (Akiyama et al. 2005), biofilm formation (Yuan et al. 2015), and pathogen suppression (Liu et al. 2014). Therefore, we can conclude that the identification and perception of plant signals by PGPR is the foremost step in establishing beneficial/harmful PRM interactions. Accordingly, plants can be genetically altered to synthesize specific signaling compounds to recruit the valuable groups of PGPR in agriculture.

### Microbe to microbe signaling network in the rhizosphere

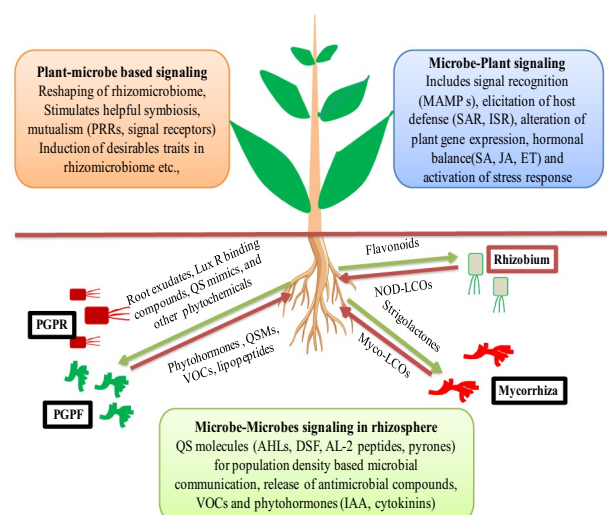
Microbe to microbe signaling exchange and communication within the root microbiome community mainly occurs through the quorum sensing (QS) mechanism. QS-based intraspecific microbial interactions control the expression and regulation of specific gene functions in a population density-dependent mode (Podile et al. 2008). The QS begins with the extracellular release of auto-inducers (act as signal molecules) into the surrounding environment. In Gram-negative bacteria, two components of the S regulatory system are transcriptional activator protein (R protein) and the autoinducer molecule (AI). Conversely, *N*-acyl homoserine lactones (AHLs) primarily function as AI in some other Gram-negative bacteria. The AI-2 is a boron-containing universal QS signal molecule in diverse Gram-negative and Gram-positive bacteria (Rosier et al. 2018). The AHL synthesizing organisms are primarily involved in root colonization, intra-kingdom communication system, and influencing root microflora (Lugtenberg and Kamilova 2009). Few strains of gram-negative rhizobacteria, e.g., *Burkholderia* spp. and *Stenotrophomonas maltophilia* may communicate through Diffusible-signal factor (DSF) as a signaling compound (Ryan et al. 2015). Many Gram-positive bacteria residing in the root-soil zone use peptides as QS signaling molecules; these molecules probably perform different roles both at the intra- and interspecies communication level (Venturi and Keel 2016). Besides these, numerous fungi interact with bacterial species via the secretion of multiple QS molecules such as  $\gamma$ -butyrolactone,  $\gamma$ -hepta-lactone, farnesol tyrosol, and dodecanol (Bukhat et al. 2020). Besides the well-known role of QS molecules in microbial communication systems and gene expression regulation, they are also vital in the symbiotic PRM interactions, plant root and

growth promotion, abiotic and biotic stress response, immunity priming, and hormonal and related metabolic modulation (Bukhat et al. 2020). Furthermore, they can modulate various phenotypic behaviors in rhizobacteria, such as rhizosphere competence, conjugation, biosynthesis of lytic enzymes, and secondary metabolites. Likewise, certain bacteria can quench auto-inducer signals produced by root pathogens, leading to their growth suppression and virulence inhibition (Morello et al. 2004).

The production of VOCs is a vital attribute of many microorganisms. They are usually small molecules (100–500 Da) such as alkenes, ketones, benzenoids, alcohols, aldehydes, terpenes). Microbial VOCs also play vital roles in microbe-microbe and plant-microbe interplay in the rhizosphere (Bitas et al. 2013). They act like chemical weapons by showing antimicrobial activity; otherwise, they can interfere and affect other QS-based communication systems (Bitas et al. 2013; Schmidt et al. 2015). Additionally, microbial VOCs can function as intra- and interspecies signals to coordinate gene expression and influence microbial behaviors such as virulence, biofilm formation, and stress tolerance (Bitas et al. 2013). Inter and intra communication network in rhizosphere microbiome-plant interaction has been given in Fig. 1.

### Rhizosphere microbiome mediated enhanced plant health and resilience under abiotic and biotic stresses

Root and soil allied microbes provide essential host functions that contribute directly to plant fitness, productivity, and resilience to biotic and abiotic stresses. Such microbiome, directly and indirectly, impacts plant performance



**Fig. 1** Inter and intra communication network in rhizosphere microbiome-plant interaction

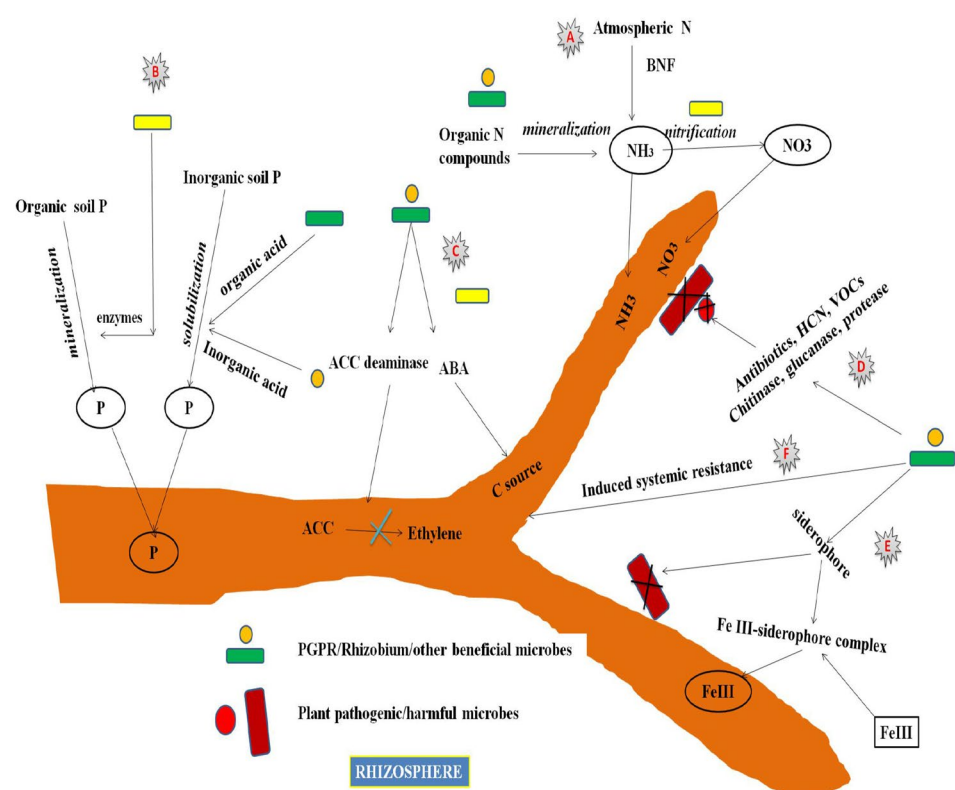
and productivity. Numerous plant-PGPR interactions and many benefits offered by rhizosphere inhabiting PGPR to host plants have been depicted (Fig. 2).

## Rhizosphere microbiome enhancing the uptake of nitrogen (N)

In the environment, bioconversion of atmospheric N into plants usable ammonium ( $\text{NH}_4^+$ ) is mediated by the nitrogenase enzyme complex present in symbiotic and associative mutualistic N-fixing microbes, called diazotrophs (Dellagi et al. 2020). Almost 70% of land N generated in  $\text{NH}_4^+$  are derived from legume-rhizobia symbiosis and can provide up to 90% of N required by legume crops (Fowler et al. 2013; Lehnert et al. 2018). In addition, associative N-fixing bacteria also provide N nutrition to plant. The promising bacterial genera are *Azotobacter*, *Pseudomonas*, *Azospirillum* and *Herbaspirillum*, *Bacillus*, *Burkholderia*, *Achromobacter*, *Klebsiella*, *Gluconobacter*, and *Acetobacter* (Saritha and Kumar 2019; Dellagi et al. 2020). Usually, the associative N fixers are less efficient in N fixation than legume root nodulating bacteria. However, their N fixing ability could be enhanced by genetic engineering (gene mutation or introgression of constitutive promoters) to regulate the production and secretion of  $\text{NH}_4^+$  (Ambrosio et al. 2017), as reported in wheat (Santos et al. 2017).

Indirectly, rhizobacteria increase plant N bioavailability by modulating root surface area and morphology. In supplying N, some rhizobacteria may alter the host root mineral uptake and translocation systems (Calvo et al. 2019). For instance, rhizosphere colonizing *Bacillus* activated the expression of genes implicated in  $\text{NH}_4^+$  and nitrate ( $\text{NO}_3$ ) assimilation in *A. thaliana* (Calvo et al. 2019). A substantial increase in the transcript levels of  $\text{NO}_3$  transporters (*NRT1* and *NRT2*) and  $\text{NH}_4^+$  transporter (*AMT1*), accompanied by elevated N absorption and plant growth, was observed. Biological N fixation and its uptake involve biochemical, molecular, and physiological components, especially under challenging environmental conditions. The specific role of a unique non-coding (nc) RNA molecule at the post-transcriptional stage and modulation of numerous physiological processes have been described (Fan et al. 2015). This ncRNA aids in the N-fixing activities of rhizobacteria under various abiotic conditions. Their presence in the bacterium *Pseudomonas stutzeri* A1501 had given insights into the regulatory pathways of the dinitrogenase enzyme complex under a challenging environment (Zhan et al. 2016). The ncRNA present in the core bacterial genome (NfiS) modulates the expression of different gene clusters, including nitrogen-fixing genes (*nif*). NfiS trigger the expression of regulatory cascade genes such as global nitrogen activator (*RpoN*), RNA polymerase sigma factor (*RpoS*), *nif*-specific activator (*NtrC*), and transcriptional promoter of all *nif* operons

**Fig. 2** Schematic diagram showing plant-beneficial microbiome interactions and key benefits offered by rhizosphere colonizing microbiome to the host plants. Plant associated microorganisms directly or indirectly contribute to plant growth and support mainly through (A) acquisition of nitrogen (N) via its biological fixation and mineralization of organic sources, (B) supply of P nutrition through solubilization and mineralization of soil P, (C) production of phytohormones and stress-responsive growth hormones, (D, E) direct growth suppression of phytopathogens and activation of host defense system, and (F) production of siderophore for the acquisition of soil iron and competitive suppression of plant pathogens



(*Nif A*) genes and post-transcriptional regulation of dinitrogenase *nifK* mRNA (Zhan et al. 2016). Besides, several other rhizobial genes include *groEL* (heat shock protein), *otsA* (trehalose-6-phosphate synthase), *clpB* (chaperone), and *rpoH* (transcriptional regulator), which function in the survival, stress tolerance, and symbiosis with a legume (da-Silva et al. 2017). Several vital genes encoding heat shock proteins (HSPs) were identified in *Bradyrhizobium japonicum* and *S. meliloti* induced legume root nodules. Under water-deficit stress, gene *MtCAS31* (*Medicago truncatula* cold-acclimation-specific 31), protecting the leghemoglobin MtLb120-1 from thermal denaturation, was only found in *M. truncatula* root nodules and was absent in the mutant genotype (Li et al. 2018b). Rhizobia with altered gene functions for specific genes show improved N fixing ability and host plants' survival under harsh agro-environment conditions. Tsyganov et al. (2020) reported that expression of metallothionein genes (*PsMT1* and *PsMT2*) from pea in *Rhizobium leguminosarum* improved tolerance to Cd toxicity and nodules development. Symbiotic N fixation by salt loving rhizobia is pivotal in balancing plant requisite for N under salt stress conditions. Salt-tolerant PGPR such as *Bradyrhizobium* sp., *actinomycetes* sp., and soil bacilli (*Bacillus* and *Paenibacillus graminis*) accelerate the activity of enzymes linked with glutamine synthetase/glutamine oxoglutarate aminotransferase (GS/GOGAT) pathways (required for the integration of  $\text{NH}_4^+$  into amino acids) under salt stress (Santos et al. 2018). Under apigenin (flavonoid) and salt stress, the proteome profile of *Rhizobium tropici* CIAT 899 revealed the molecular responses with the identification of several candidate proteins associated with bacterial adaptation to environmental conditions and nodulation process (Maximiano et al. 2021). Several proteins implicated in N compound transport and metabolism appeared differentially plentiful, emphasizing the ability of these stresses to stimulate metabolic changes favoring the establishment of favorable PRM association.

Usually, heavy metals hamper legume growth, rhizobial nodulation, dinitrogenase activity, and N fixation performance (Fagorzi et al. 2018). The presence of heavy metals (Cu(II) and Zn(II)) reduced dinitrogenase activity and nodule formation in *Medicago lupulina*. In contrast, whereas co-inoculation of *M. lupulina* with *Rhizobium radiobacter* and *Ensifer meliloti* mitigated heavy metal stress and considerably improved dinitrogenase activity and plant biomass (Jian et al. 2019). Many PGPR, including rhizobium strains, depicts different levels of tolerance to several abiotic stresses. For example, several PGPR strains (*Rhizobium* spp. strain UFSM-B74, *Bradyrhizobium* spp. strains UFSM-B53 and UFSM-B54, and *Burkholderia* spp. strain UFSM-B33/UFSM-B34) isolated from *Macroptilium atropurpureum* and *Vicia sativa* are tolerant to alkaline (pH = 9.0) and acidic (pH < 3.0) (Ferreira et al. 2018). These strains also show

differentially tolerance capacity to high metal concentrations in the order of Cr > Cd > Zn > Ni > Cu. Recently, the role of legume plants specific protein in a symbiotic relationship with the rhizobium, especially under abiotic stress conditions, has been demonstrated. Using genome-wide analysis and expression profiling, Boubakri et al. (2021) revealed the presence of distinctive isoforms of H-type thioredoxins (Trxs) family proteins in *Phaseolus vulgaris* (Pv), associated with symbiotic N-fixing performance of *Rhizobium gallium* 8a3 and abiotic (salt and oxidative) stresses response. RT-qPCR analysis showed that PvTrxh genes were highly expressed in the nodule primordium (NP) during nodule organogenesis. Moreover, specific PvTrxh isoforms (PvTrxh3 and h5) were highly upregulated in inoculated plants and their expression patterns in NP correlated positively with N-fixing efficiency. On the contrary, distinctive PvTrxh isoforms were upregulated in plant leaves under salt and drought stress (Boubakri et al. 2021).

### Rhizosphere microbiome in the supply of phosphorous nutrition

Many PGPR can convert different inaccessible forms of soil P to the plant-available forms through the solubilization and mineralization process. Inorganic sources of soil P(iP) are solubilized by the species of *Achromobacter*, *Agrobacterium*, *Azotobacter*, *Beijerinckia*, *Bacillus*, *Burkholderia*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Rhizobium*, *Pseudomonas*, *Serratia*, and fungi (*Aspergillus*, *Penicillium*, *Fusarium*, *Chaetomium*, and *Cephalosporium*) (Sharma et al. 2013; De Boer et al. 2019). In solubilizing iP, rhizobacteria discharge proton H<sup>+</sup> to their outer surface for cation uptake (Rodríguez and Fraga 1999). They can also release extracellular organic acids (acetic, lactic, isobutyric, oxalic, citric, succinic, gluconic acid, and 2-ketogluconic acid) (Zhao and Zhang. 2015; Naraian and Kumari 2017). Once diffused exterior to the cell surface, the carboxyl (COOH) and hydroxyl (OH) residue solubilize iP by providing metal-binding proton and anion (Chhabra et al. 2013).

In bacteria, the pyrroloquinoline quinone (PQQ), a cofactor of the glucose dehydrogenase enzyme (Ge et al. 2015; Chen et al. 2016), is encoded by the *pqq* operon. The *pqq* operon consisting of core genes (such as *pqqA*, *pqqC*, *pqqD*, and *pqqE*) are vital for the bacterial P solubilizing ability (Li et al. 2014; Oteino et al. 2015; An and Moe 2016). iP solubilization involves the differential expression of numerous microbial genes. Through transcriptomic analysis, Zeng et al. (2017) demonstrated that the 46 genes linked with cell growth and P-solubilization in *Burkholderia multivorans* WS-FJ9 was differentially regulated in response to different levels of external P. Particularly, genes encoding glycerate kinase (linked with glucose metabolism), 2-oxoglutarate dehydrogenase (involved in organic acids production), and

histidine protein kinase PhoR (implicated in the signaling process) were overexpressed under P deficiency (Zeng et al. 2017). Stress-tolerant PGPR effectively solubilizes P and improves plants health by modulating gene regulation profiles under adverse growth conditions. Upon inoculation, the salt-tolerant P solubilizing PGPR *Pseudomonas korensis* MU2 upregulated the salt-responsive genes (*GmST1*, *GmSALT3*, and *GmAKT2*) in soybean plants (Adhikari et al. 2020). Bacterial inoculation leads to the improved P and silicate (Si) uptake, antioxidant system, and salt stress tolerance by lowering the Na<sup>+</sup> ion influx by 70% and increasing K<sup>+</sup> uptake by 46%. Bacteria can also enzymatically convert soil organic P into iP during the mineralization process. Under salinity stress, some PGPR strains can modulate the expression of certain key genes related to phosphate transport and improve PO<sub>4</sub> in host plants (Mishra et al. 2021). In salt-tolerant PGPR, genes related to organic acid production and phosphatase activity were over-expressed, leading to the increased solubilization of iP. For instance, inoculation of the bacterium *Pseudomonas putida* MTCC 5279 showed enhanced acidic phosphatase activity under salinity and P-starved conditions (Srivastava and Srivastava, 2020).

The soil P mineralization is chiefly catalyzed by (a) non-specific acid phosphatases, predominantly represented by acid and alkaline phosphatases (phosphomonoesterases), which hydrolyze phosphodiester and phosphoanhydride bonds, (b) phytases (Myo-inositol hexakisphosphate phosphohydrolases), capable of converting phytate into iP fraction, and (c) C–P lyases and phosphonatasases, able to slice C–P bond of organophosphonates (Sharma et al. 2013; Jain and Sapna 2016; Alori et al. 2017). Certain strains of *Enterobacter*, *Serratia*, *Citrobacter*, *Rhizobium*, *Pseudomonas*, and *Proteus* are potent phytase producers (Kumar et al. 2016). Using genetic engineering, phytase encoding genes were overexpressed in a few roots colonizing *proteobacteria* to mineralize orthophosphate from phytate and make it available for growth of the *A. thaliana* plants (Shulze et al. 2019). The study concluded that DNA synthesis strategy could be helpful to design PGPR strains with novel P-metabolizing capabilities. Phosphatase synthesizing phosphobacteria, i.e., *Klebsiella* spp. strain RC3 and RCJ4, *Stenotrophomonas* spp. RC5, *Enterobacter* spp. RJAL6 and *Serratia* spp. RCJ6 can effectively provide P nutrition and support plant growth under P deficiency and aluminum toxicity conditions (Barra et al. 2018). In addition to PGPR, the particular rhizobial strain also solubilizes unavailable soil iP for plant uptake. In addition, bacteroids formed in root nodules also require P for their metabolism. The high-affinity phosphate transporter PstSCAB is well-known for enhancing the symbiotic efficacy of the *Sinorhizobium fredii*-soybean (Hu et al. 2018). Under the P-starvation conditions, phoCDET genes encode the ABC-type transport system in *Sinorhizobium meliloti*, leading to enhanced uptake of iP and increased N fixation

activity (Jaiswal et al. 2021). In P-limited soils, rhizobia solubilize soil iP via production of gluconic acid under the control of the PQQ genes (Yadav et al. 2020). In rhizobia, the gene *gcd* encoding quinoprotein glucose dehydrogenase (PQQGDH) is crucial for the release of organic anions to solubilize iP (Jaiswal et al. 2021). Thus, given the central roles of P in both plant and rhizobacterial metabolism, screening for P-solubilizing traits in N-fixing rhizobia can be a rational approach for mitigating the adverse effects of P stress on plants.

### Improved soil potassium and minor plants nutrients by rhizospheric microorganisms

Several rhizosphere microorganisms facilitate plant uptake of soil K. Bacterial species such as *Bacillus mucilaginosus*, *Bacillus edaphicus*, *Pseudomonas* spp., *Acidithiobacillus ferrooxidans*, *Bacillus circulans*, *Paenibacillus* spp., and *Burkholderia* spp. are well recognized K solubilizing bacteria (KSB) (Sheng 2005; Liu et al. 2012). As discussed by Etesami et al. (2017), KSB solubilizes soil K mineral by different mechanisms, including: (i) lowering the pH, (ii) increasing chelation of the cations bound to K mineral, and (iii) acidolysis of the nearby area. Rhizosphere inhabiting KSB modulates host plants' molecular, biochemical, and physiological aspects, especially under challenging conditions. Recently, KSB solubilizing and other plant growth-promoting (PGP) traits holding bacterium *Bacillus amyloliquefaciens* B11 improved chlorophyll, sugar, amino acid, SA, proline, and antioxidant activities of pepper plants under salinity and drought stress (Kazerooni et al. 2021). Furthermore, differential gene expression was observed, including the up-regulation of *XTH* genes and downregulation of *WRKY2*, *PTII*, *BI-1*, and binding immunoglobulin protein (*BiP*) genes. Using growth characteristics, enzyme activity, and gene expression analysis, Feng et al. (2019) revealed the positive impacts of KSB and photosynthetic bacterial inoculation on the superior performance of antioxidant enzymes and their expression related genes (SOD, CAT, APX, and PPC) in maize plants under salinity stress. These results indicate that these bacteria can effectively increase maize productivity in saline-alkali soil (Feng et al. 2019).

Besides, soil microbes also make bioavailability of other trace elements such as iron (Fe), zinc (Zn), sulfur (S), and Si to the plants (Adesemoye et al. 2009; Hafeez et al. 2013). Microbially produced iron-chelating siderophores, gluconate, or the derivatives of gluconic acids, e.g., 2- keto-gluconic acid, 5-keto-gluconic acid, and other organic acids facilitate the mineralization of these minor elements (Tariq et al. 2007; Saravanan et al. 2011). The siderophore-mediated uptake of Fe is the most encountered mode adopted by rhizobacteria in supplying soil Fe to plants (Kramer et al.

2020). Microbial siderophores such as enterobactin, pyoverdine, and ferrioxamines (produced by bacteria), and ferriochrome (produced by fungi) chelates ferric ion ( $\text{Fe}_3^+$ ) and reduce it to the soluble ferrous ion ( $\text{Fe}_2^+$ ) inside the cytoplasm. The siderophore pyoverdine-producing bacterium, *Pseudomonas fluorescens* C7R12, regulates the expression of about 2000 genes associated with Fe acquisition, growth, and priming host immunity in *A. thaliana* (Trapet et al. 2016). Gene expression profile revealed that the several Fe uptake linked genes were up-regulated. Conversely, host defense-related several genes such as transcription factors *ERF*, *MYB*, *WRKY*, *SA* gene (such as *AT5G24210*, encoding lipase class 3 family protein), and an abscisic acid (ABA)-related gene, encoding lipid transfer protein LTP3, were down-regulated (Trapet et al. 2016). Several PGPR can boost the nutrient availability and mineral density in the edible portion of the crop. As reported by Sathya et al. (2013), 19 different PGP actinobacteria drastically increased seed mineral density for Fe, Zn, calcium (Ca), Cu, manganese (Mn), and magnesium (Mg) in chickpeas. The qualitative RT-PCR analysis revealed that the increased mineral concentrations were possibly due to the synthesis of microbial siderophore, as genes encoding siderophore were highly expressed (up to 1.4 to 25-fold). Soil microbiome also triggers nutrient uptake and transport in the plants. The crucial roles of the mineral transporters system in the translocation of soil nutrients from shoot to grains have been reported. For example, Zn and Fe regulated transporters like ZIP family proteins (ZIP), mainly concerned with the Zn and Fe-regulated transporter (*ZRT/IRT*), translocate these micronutrients in wheat (Evens et al. 2017), maize (Xu et al. 2010), and rice (Ishimaru et al. 2005). Using the qRT-PCR approach, the role of Zn-solubilizing bacterium *Enterobacter cloacae* ZSB14 on the modulation of genes encoding ZIP in rice under Fe toxicity and poor conditions was revealed (Krithika and Balachandar 2016). Following bacterial inoculation, *OsZIP1* and *OsZIP5* genes were up-regulated, while, *OsZIP4* gene was down-regulated, leading to the assimilation and metabolism of Zn in the plant shoots and roots. Similarly, under Zn deficiency, inoculation of barley with roots colonizing AMF, *Rhizophagus irregularis* significantly and consistently up-regulated expression of the *HvZIP13* gene encoding ZIP transporters in the roots (Watts-Williams and Cavagnaro 2018). Subsequently, positive regulation of this gene resulted in the augmented uptake of Zn in grain and straw. Legume crops also benefit from the microbiome facilitated enhanced mineral uptake. Gopalakrishnan et al. (2016) demonstrated the potential of different rhizobacterial strains such as *Pseudomonas plecoglossicida* SRI-156, *Brevibacterium antiquum* SRI-158, *Bacillus altitudinis* SRI-178, *Enterobacter ludwigii* SRI-211, *E. ludwigii* SRI-229, *Acinetobacter tandoii* SRI-305, and *Pseudomonas monteilii* SRI-360 in improving accessibility of minerals in chickpeas

and pigeon pea. Following inoculation, legume grains exhibited improved mineral contents, e.g., Zn (up to 23 and 5%), Fe (up to 18 and 12%), Ca (up to 22 and 11%), copper (up to 19 and 8%), and Mn (up to 2 and 39%) in chickpea and pigeon pea, respectively. These studies sum up the functions of various PGPR in the bioaccessibility of numerous soil nutrients to the plants. These findings could assist in the design and development of microbial inoculants to alleviate the nutrient deficiency of soil and plants.

### Rhizosphere microbiome mediated phytohormones production and plant growth regulation

Diverse rhizosphere microbiome synthesizes key phytohormones to support plant growth, metabolism, and overall development. Different phytohormones directly modulate cellular, biochemical, physiological, and morphological processes involved in plant development (Shah and Daverey 2020).

### Auxins

Among the phytohormones, auxins represent one of the most predominantly occurring and recognized hormones. It is well known that the IAA/auxin as phytohormone is produced by almost 80% of the rhizosphere inhabiting PGPR. Among PGPR, *Azospirillum* spp., *Azotobacter* spp., *Aeromonas* spp., *Burkholderia* spp., *Enterobacter* spp., *Pseudomonas* spp., and *Rhizobium* spp., are the main PGPR capable of IAA synthesis (Hariprasad and Niranjana 2009; Rajkumar et al. 2012; Park et al. 2017a, b). IAA is synthesized from the tryptophan (as a precursor molecule via the tryptophan-independent pathway (Spaepen and Vanderleyden 2011); primarily utilize the indole-3-pyruvate (IPyA) pathway (Ma et al. 2011). In the IPyA pathway, the indole-3-pyruvate decarboxylase enzyme converts IPyA to the indole-3-acetaldehyde, an intermediate precursor of IAA. In addition to IAA, some PGPR may deliver more than one kind of growth modulation compound to their host plant, e.g., indole-3-lactic acid, indole-3-acetaldehyde, indole-3-acetamide, and indole-3-ethanol (Spaepen and Vanderleyden 2011; Patten et al. 2013).

Usually, plants synthesize IAA/auxin when exposed to different environmental signals such as temperature, heavy metals, and pathogen infection (Zhao 2018). To enhance the drought response, auxins modulate the ROS metabolism, root structure, metabolic equilibrium, and several ABA-responsive genes (such as *DREB2A*, *DREB2B*, *RD22*, *RD29A*, *RD29B*, and *RAB18*) (Shi et al. 2014). In recent studies, Zhang et al. (2020a, b) demonstrated that exogenous IAA treatment significantly mitigated drought stress in white clover via differential expression profile of auxins and drought-linked genes. For instance, moisture



deficit stress-linked several genes (*bZIP11*, *DREB2*, *MYB14*, *MYB48*, *WRKY2*, *WRKY56*, *WRKY108715*, and *RD22*) and auxin-responsive genes (*GH3.1*, *GH3.9*, *IAA8*) were upregulated, while genes responsible for leaf senescence (*SAG101* and *SAG102*) and auxin responding (*GH3.3*, *GH3.6*, *IAA27*) were down-regulated (Zhang et al. 2020a, b). Further, auxins upregulate the expression of *IAA8* that is responsible for the formation of the lateral roots, and downregulate the expression of the *SI-IAA27* gene implicated in growth and root developmental activity. Auxin-responsive gene *TaSAUR75* enhances the expression of genes *AtRD26* and *AtDREB2*, which are crucial in plant growth and development during moisture-stressed conditions (Guo et al. 2018). Briefly, auxin is involved in the abiotic stress mitigation via activation of other stress-linked hormones and the production of ROS.

Certain rhizobacteria can sufficiently synthesize IAA by utilizing its precursor molecules from root exudate compounds accumulated in the rhizosphere. As reported by Liu et al. (2016), cucumber rhizosphere bacterium *B. amyloliquefaciens* SQR9 produced bountiful IAA by utilizing rhizodeposit tryptophan and offered benefits to host plants. Further, the tryptophan transport (*Csa024547*) and IAA biosynthesis genes were over-expressed in the host plant (Liu et al. 2016). The elevated level of IAA exerts stimulating effects on the growth, biomass, and yield in many crops under normal as well stressed conditions, e.g., wheat growth promotion by *B. licheniformis* HSW-16 under salt (Singh and Jha 2016) and similarly by *Enterobacter* spp. strain NIASMVII (Sorty et al. 2016) increased biomass in *Trifolium repens* by *Pseudomonas putida* and *Bacillus megaterium* (Marulanda et al. 2009), and grain yield in chickpea by *Serratia* spp. (Zaheer et al. 2016). Furthermore, IAA synthesizing PGPR may elicit a plant defense system to alleviate the abiotic stress-induced adverse effects. As observed in *Vinca rosea* plants, the IAA-synthesizing bacterium, *B. megaterium*, promote plant growth and ameliorate nickel stress through activation of metabolic biosynthesis pathways related to antioxidative enzymes (catalase (CAT), superoxide dismutase (SOD), peroxidase (PO), and ascorbate peroxidase (APO), phenolics, and flavonoid (Khan et al. 2017). Along with IAA, salt-tolerant, organic acid, and EPS producing PGPR strains, *Bacillus aryabhatai* ALT 29, and *Arthrobacter woluwensis* ALT43 mitigated the salinity stress and increased plant growth, chlorophyll, and biomass in soybean under NaCl (80 mM, 160 mM, and 240 mM) stress (Khan et al. 2021). Overall improvement in plants performance was due to regulation of endogenous phytohormones, antioxidants, ion uptake, and gene expression (*GmFLD19* and *GmNARK*) under salinity (Khan et al. 2021). The synthesis of auxin/IAA is a familiar trait in many *Rhizobium* species. *Rhizobium* alters the concentration of auxins in the roots and nodules, thereby leading to strong alterations in the root system structure, such as improved

growth and the number of lateral roots. These structural root alterations may influence root nodulation and nodulation efficiency under normal as well as stressed environments (Concha and Doerner, 2020). A recent study by Tulumello et al. (2021) showed that rhizobium bacterium *Rhizobium alarii* GBV030 promote plant growth and minimize the adverse effects of moisture stress on rapeseed growth. Phytostimulation by rhizobium is possibly due to the synthesis of phytohormones, regulating the hormone balance of the host plant, or the production of biomolecules improving the plant availability of soil nutrients (Olenska et al. 2020).

## Cytokinins

Cytokinins are another class of phytohormones synthesized by many soil microbiomes. The prominent bacteria synthesizing cytokinins are *Azotobacter* spp., *Rhizobium* spp., *Pantoea agglomerans*, *Rhodospirillum rubrum*, *P. fluorescens*, *Bacillus subtilis*, and *Paenibacillus polymyxa*. On average, almost 90% of rhizobacteria produces cytokinin-like plant growth stimulatory compound in vitro. Several bacteria colonizing roots of *Coleus forskohlii*, such as *Pseudomonas stutzeri* MTP40, *Pseudomonas putida* MTP50, and *Stenotrophomonas maltophilia* MTP42 secrete plant growth-promoting cytokinin molecules (Patel and Saraf 2017). The exact modes of cytokinin biosynthesis in bacteria are not precise. However, the crucial role of isopentenyl transferase (encoded by an *ipt* gene) in the cytokinin biosynthesis pathway is reported. This enzyme converts isopentenyl moiety from dimethylallyl diphosphate (DMAPP) to adenosine monophosphate (AMP), an initial step in cytokinin biosynthesis. Bacteria can also initiate cytokinin synthesis by transferring isopentenyl moiety from 1-hydroxy-2-methyl-2(E)-butenyl 4-diphosphate (HMBDP) to AMP (Wong et al. 2015).

In *A. thaliana* plants, cytokinin-based signaling drives primary root growth, supports plant growth, and alters root architecture (Naulin et al. 2020). Also, cytokinin is an essential growth hormone in adapting plants to various environmental conditions (drought, temperature, salt, osmotic, and nutrient stress) (Cortleven et al. 2019). Cytokinins can augment plants tolerance limits against osmotic stress (Karunadasa et al. 2020). For instance, trans-zeatin, cytokinins obtained from the root of *A. thaliana*, guard the plant against photoperiod-induced stress conditions (Frank et al. 2020). Under osmotic stress, cytokinins synthesis reduces ROS-induced damages, lipid peroxidation, defer leaf senescence, thereby improving stress tolerance (Gujjar and Supaibulwatana 2019). Further, up and down-regulation of cytokinins enhance plant tolerance under moisture deficit conditions. During the abiotic stress, cytokinins biosynthetic gene, *ISOPENTENYL TRANSFERASE*, is overexpressed, leading to improved antioxidant activity, root growth, and

drought tolerance capability of plants (Xu et al. 2016). During moisture deficiency, the plant shows a substantial build-up of cytokinins in root tissues due to a decreased activity of *CYTOKININ OXIDASE/DEHYDROGENASE* (Havlová et al. 2018). Therefore, we can conclude that cytokinins activate numerous signaling reactions, secretory proteins, and antioxidants to cope with harsh conditions.

Several PGPR can enhance levels of cytokinins concentration in soil solution and thereby, the growth promotion of plants growing there. Similar to cytokinins applied exogenously, plants inoculated with cytokinins producing bacteria support plant growth similarly (Liu et al. 2013). For instance, the increased root and shoot dry biomass of *Platyclusus orientalis* by cytokinins producing *Bacillus subtilis* was reported by Liu et al. (2013). Plants exposed to challenging agricultural environments may also benefit from cytokinins-producing bacteria. Cytokinins synthesizing bacterium *Bacillus aryabhatai* strain SRB02 augment soybean growth and development under the abiotic-stressed environment (Park et al. 2017a; b). Some bacteria-produced cytokinins perform a dual role in nutrient supply and priming host immunity in response to biotic and abiotic stresses (Akhtar et al. 2020). The priming host immunity against pathogen was reported in the *A. thaliana*-cytokinins producing *Bacillus megaterium* interaction system (Grosskinsky et al. 2016). Under drought stress, cytokinins producing *Bacillus* sp. significantly increased cytokinins content in both shoots and leaves, accompanied by increased biomass and root sink strength (Arkhipova et al. 2007). A similar delay in drought-incited senescence was noticed in alfalfa plants inoculated with cytokinins-synthesizing bacterium *Sinorhizobium meliloti* (Xu et al. 2012). The over-production (up to five times) of cytokinins can be achieved via transformation through the expression of the *Agrobacterium* IPT gene. Under drought conditions, cytokinins producing *Azotobacter chroococcum* lead to the accretion of stress response hormone, which degrades stress induced ROS, thereby mitigating the adverse effect of drought (Grover et al. 2011). Recently, the cytokinins producing bacterium *Methylobacterium oryzae* considerably increased plant growth, physiological traits, and drought tolerance in lentils (Jorge et al. 2019).

## Gibberellins

Gibberellins (GA) can mitigate abiotic stress and affect other physiological processes of plants. In plants, GA plays a vital role in lowering the adverse effects of abiotic stress-induced injuries. In salt-affected rice plants, the exogenous application of GA up-regulates lipid biosynthesis (Liu et al. 2018). Upon exposure to zinc oxide nanoparticle stress, GA application has reduced the accumulation of zinc and ROS, resulting in superior photosynthesis, biomass, nutrient quality, and grain

yield in wheat (Iftikhar et al. 2019). GA enhances tolerance to temperature-induced stress by changing the cell wall and plastid structure in tomato plants (Gamel et al. 2017). Some studies have shown that the reduced GA levels increase drought tolerance in plants via inhibiting plant growth and development. Several genes, such as the *AtGAMT1* gene and *SIDREB*, can be overexpressed to generate the inactive GA or downregulate GA biosynthetic genes (Yadav et al. 2020). The lower level of plant GA promotes the drought tolerance in tomatoes by restricting internode elongation and leaf expansion. Such plants usually have smaller leaves and high stomatal intensity, which helps in lowering the transpiration rate (Yadav et al. 2020). So, we can say that GA negatively regulates the moisture deficit stress compared to other plant hormones.

The production of gibberellins (GA)-like substances have been reported in *Azospirillum* spp., *Acetobacter diazotrophicus*, *Bacillus* spp., *Herbaspirillum seropedicae*, and *Rhizobium* spp. (Nagel et al. 2018). Around 136 different chemical structures of GA have been identified. Rhizobacteria predominantly synthesize gibberellic acid (GA3) as the primary GA-like substance. In bacteria, the GAs biosynthesis pathway begins from the geranyl-geranyl diphosphate (GGPP) as a starting compound and involves a sequence of reactions catalyzed by several cellular enzymes (Nett et al. 2017; Salazar-Cerezo et al. 2018). The exact functions of GA in synthesizing microbes are not precise; however, they probably act as a signaling molecule during mutualism with host crops, e.g., in *Rhizobiaceae*-legumes symbiotic association (Nett et al. 2017). Numerous reports have confirmed that microbial-produced GA positively impacts plant growth and development. For instance, promotion of root growth by different *Azospirillum* strains (Revolti et al. 2018), increased shoot length and biomass in rice and oriental melon by GA and IAA synthesizing *Enterococcus faecium* LKE12 (Lee et al. 2015), increased growth and salinity tolerance in tomato by GA4 producing *Sphingomonas* sp. LK11 (Halo et al. 2015) was correlated positively to the different GA produced by the rhizobacteria. The promotion of tomato growth in salinity was correlated positively with decreased lipid peroxidation, PO, CAT, PPO, and enhanced activity of glutathione (Halo et al. 2015). GA producing *Leifsonia xyli* strain SE134 sustain the growth of tomato and most possibly trigger plant resistance to Cu (II) induced stress (Kang et al. 2017). The increased GA synthesis was accompanied by elevated glutamic acid, glycine, phenylalanine, threonine, proline, and arginine, which substantially influenced plant biomass (Kang et al. 2017). Further, the total polyphenol and flavonoid correlated with reduced SOD activity, the most probable mechanism in Cu (II) stress mitigation (Kang et al. 2017). Similarly, a wide array of GAs (GA1, GA3, GA5, GA8, GA19, GA24, and GA53) producing bacterium *Bacillus tequilensis* SSB07 increases plant length and biomass

under high-temperature stress (Kang et al. 2019). The bacterium *B. tequilensis* SSB07 imparts heat stress resistance mainly via phytohormonal modulation and upregulation of JA and SA under elevated temperature (Kang et al. 2019). Besides stress alleviation, phytohormone-producing rhizobacteria enhance plants performance and development. For instance, GA, auxin, and cytokinins producing bacteria *Pseudomonas aeruginosa* PM389, *Pseudomonas aeruginosa* ZNP1, *Bacillus endophyticus* J13, and *Bacillus tequilensis* J12 mitigated the adverse effects of drought stress on plants, as confirmed by the increased fresh and dry weight and water content in *A. thaliana* plants (Ghosh et al. 2019).

### Abscisic acid and ethylene

ABA is another stress-induced compound of microbial origin that modulates plant roots hydraulic conductivity, biochemical/physiological processes, and transcription factors of many stress-responsive genes. Plants build up ABA in stress conditions that elicit a response to cope with the adverse environmental conditions. Plant exposed to moisture deficiency synthesize ABA in their roots and translocate to the upper portion to trigger drought adjustment mechanisms such as growth diminution and stomatal closure (Qi et al. 2018). Further, ABA activates the expression of several stress-responsive genes that mitigates the negative impacts of suboptimal conditions. For instance, ABA-activated SnRK2s, implicated in the phosphorylation of the type-A ARR5, aids in the enhanced stress response of plants (Huang et al. 2018). Several overexpressed genes such as IbARF5 up-regulate ABA biosynthetic genes (IbZEP, IbNCED, and IbABA2) and confer drought tolerance in transgenic *A. thaliana* (Kang et al. 2018). Further, the positive regulation of REL1 directs the ABA biosynthetic pathway to modulate moisture deficit stress in plants (Liang et al. 2018). Additionally, SAPK2 is the primary regulator of ABA-mediate development processes in several plants. SAPK2 is involved in the upregulation of the expression of numerous stress-linked genes, including OsOREB1, OsRab16b, OsLEA3, and OsRab21, and OsbZIP23, during stress induced by abiotic factors (Lou et al. 2017). These stress-regulated genes may be a probable target for the plant's genome engineering to make them more stress adaptive.

Regarding microbe-mediated stress management, rhizosphere and soil-inhabiting many ABA-producing bacteria can lower the adverse impact of abiotic stresses on plants. For instance, the rhizobacterium *Dietzia natronolimnaea* STR1 guarded wheat plants against salinity stress by inducing over-expression of ABA-responsive genes, ion translocation, and antioxidants production (Bharti et al. 2016). Several genes associated with ABA signaling cascade (*TaABARE*, and *TaOPRI*), transcription factors (*TaMYB* and *TaWRKY*), stress-generation (*TaST*; *T. aestivum* Salt-Tolerant),

and *SOS1* and *SOS4* (Salt Overly Sensitive) pathway, and ion transporters (*TaNHX1*, *TaHAK*, and *TaHKT1*) were over-expressed. In addition, bacterial-induced osmolyte and antioxidative enzymes such as CAT, PO, APO, Mn superoxide dismutase (*MnSOD*), and glutathione peroxidase (GR) imparted salt tolerance (Bharti et al. 2016). Cold stress adaptive psychrophilic *Bacillus* spp. (CJCL2, RJGP41) harbor genes implicated in signal transduction pathways, antioxidants synthesis, and sugar-ABC transporters, lipid peroxidation, proline synthesis (Zubair et al. 2019). Bacterium-induced overexpression of these genes in wheat plants enhanced their tolerance to cold stress (Zubair et al. 2019). The bacterium also modulated the expression of genes encoding auxin, cytokinin, alpha expansion, and ethylene (ET) under cold stress. At the molecular level, especially microRNAs (miRNAs), non-coding molecules that regulate the expression of many transcriptional and post-transcriptional genes, are essential in the sustenance of plants under many abiotic stresses (Shriram et al. 2016). For instance, abiotic stress amelioration and a significant gene expression pattern in chickpeas inoculated with the ABA-synthesizing bacterium *P. putida* MTCC5279 were correlated with the expression of different miRNAs molecules (such as miR159, miR166, miR169, miR172, and miR396, etc.). This suggests a possible role of miRNAs in stress mitigation (Jatan et al. 2019). Likewise, various plant hormones synthesizing rhizobacteria such as *Pseudomonas stutzeri*, *Stenotrophomonas maltophilia*, and *P. putida* increase plants growth and performance under saline stress (Patel and Saraf 2017). The *LOX2* gene encoding lipoxygenase that regulates stress-related JA biosynthesis pathway was over-expressed (Patel and Saraf 2017).

Plants exposed to harsh abiotic and biotic stress conditions experience a higher accumulation of ET hormone. The ET causes several cellular and biochemical injuries in the plants exposed to adverse environmental conditions. In such situations, the ACC deaminase-producing rhizobacteria irreversibly convert the precursor of ET hormone, ACC, into less harmful compounds such as  $\alpha$ -ketobutyrate and ammonia. Some specific rhizobacterial compounds, such a rhizobitoxine, an enol-ether amino acid (2-amino-4-[2-amino-3-hydroxypropoxy]-Trans-3-butenoic acid), competitively inhibits the ACC synthetase and thereby reduce ET induced stress injuries (Singh et al. 2015). Several reports have confirmed that plants inoculated with PGPR producing ACC synthetase have longer roots and improved resistance levels to fungal and bacterial pathogens, as well as to waterlogging conditions. Under salt and heavy metal stress, rice plants inoculated with the ACC deaminase secreting *Pseudomonas stutzeri* A150 showed improved plant growth and tolerance to stress tolerance (Han et al. 2015). This ability was lacking in the bacterium mutant for the *acdS* gene, encoding ACC deaminase (Han et al. 2015).

Likewise, ACC deaminase possessing *Streptomyces* spp. GMKU 336 enhanced saline tolerance in rice plants by modulating differential gene expression in the host plants. Possibly, genes encoding antioxidant enzymes (*Cu/ZnSOD1*, *CATb*), osmotic balance (*BADH1*), calmodulin (*Cam1-1*), Na<sup>+</sup> transporters (*NHX1*, *SOS1*), and *acdS* biosynthesis were over-expressed in the bacterium (Jaemsaeng et al. 2018). Recently, Orozco-Mosqueda et al. (2019) generated a series of mutants of the PGPR *Pseudomonas* sp. UW4 to assess the precise functions of ACC deaminase and trehalose in conferring salinity tolerance in tomato plants. The newly generated strains included *treS* (a mutant with reduced synthesis of trehalose), *acdS/treS* (a mutant with reduced synthesis of trehalose and ACC deaminase), *OxtreS* (a mutant with an overproducer of trehalose), and *acdS* (a mutant lacking ACC deaminase activity). Interestingly, tomato plants inoculated with the wild-type strain showed increased root length, dry biomass, and chlorophyll. Conversely, the *acdS* and *treS* mutants could not offer host plants any benefits (Orozco-Mosqueda et al. 2019). Despite all this available information, our understanding of biochemical, physiological, and molecular facets of PRM interactions mediated by microbial hormones and metabolites remains limited. This area holds immense potential for discoveries on how phytohormones synthesizing phytomicrobiome offer key host functions.

### Other mechanisms adopted by PGPR to improve plants tolerance under the challenging environmental conditions

In addition to the above-discussed modes, PGPR may also impart stress tolerance through the production of EPS/biopolymer, accumulation of biocompatible osmolytes, and ion homeostasis (Paul et al. 2017). Many facets of the plant microbiome have been explored to minimize the adverse impact of unfavorable environment on the host plant via modulating molecular, biochemical, and physiological responses (Paul et al. 2017; Vejan et al. 2016). Many challenging environmental conditions alter the root microbial community and boost plant metabolism (Sangwan and Dukare 2018; Liu et al. 2020).

Drought causes a net decrease in plant and microbiome biomass. However, some types of microbe do better under moisture deficit-induced harsh conditions. Arid areas dominating drought-adapted bacteria in the plant microbiome include members from the Proteobacteria, Bacteroidetes, and Firmicutes phyla (Soussi et al. 2016). Similarly, actinobacteria or some monoderms are abundantly present in the rhizosphere and/or endosphere (Ham et al. 2018; Xu et al. 2018). This signifies the presence of co-adaptive strategies between the microbiome and host plant for ameliorating stress effects and improving nutrient uptake, metabolism,

and overall development. Apart from whole microbial cells, specific metabolites of microbial origin can also aid in making plants more resistant to moisture deficit conditions. For example, an EPS synthesized and secreted by rhizobacteria are high moisture (more than 95%) holding matrixes that improve plants tolerance by modulating cellular metabolism in dry conditions (Gouda et al. 2018). Plants exposed to EPS significantly accumulate stress-responsive osmolytes such as proline, amino acids, and trehalose. The EPS synthesizing bacterium *Pseudomonas* PS01 alleviated the negative impact of salinity stress in *A. thaliana* by modulating stress-responsive genes' expression levels (Chu et al. 2019). As observed in the *Panicum maximum* plants, microbe-mediated stress alleviation was due to the improved cell membrane stability and enhanced synthesis of photosynthetic pigments (Tiwari et al. 2018). Different stress-responsive metabolites (such as proline, abscisic acid, glycine, trehalose, and betaine) maintain membrane permeability, enzyme integrity, and protein functionalities and improve plants' stress tolerance (Manjunatha et al. 2019; Agami et al. 2016). Similarly, plants have several genes encoding stress-responsive proteins (such as PO, SOD, CAT, nitrate reductase, and GR), phenolic and flavonoids compounds, and non-enzymatic metabolites, which are usually up-regulated (El-Esawi et al. 2019; Egamberdieva et al. 2019). Under the higher salt stress, higher production of stress-responsive osmolyte metabolite, ectoine, was reported in *Halomonas* sp. SBS 10 (Kushwaha et al. 2019), further, ectoine biosynthesis genes were highly expressed. Stress mitigation in plants can also be achieved by the VOCs synthesized by the rhizosphere microbiome. For instance, *B. subtilis* GB03 synthesized VOC down-regulated the *HKT1* (high-affinity K<sup>+</sup> transporter 1) gene expression in roots and up-regulated in shoots of *A. thaliana*, thereby reducing Na<sup>+</sup> accumulation and improving stress tolerance (Saritha and Kumar 2019). Thus, rhizosphere microbiome displays promising effects to impart abiotic stress tolerance. Therefore, they can be used as agronomic management components in crop cultivation under a wide array of adverse environmental conditions. With some more recent representative studies, the functional attributes and mechanistic approaches portrayed by rhizosphere microorganisms in enhancing plant health and resilience is given in Table 1.

### Rhizosphere microbiome alleviate pathogen-induced biotic stresses

#### Mitigation of fungal pathogen-induced biotic stress

Under pathogen challenged conditions, antagonistic rhizobacteria retains control over the phytopathogens mainly by: (1) competing for restricted nutrients (especially Fe) and space; (ii) preventing virulence through antifungal

**Table 1** The functional attributes and mechanistic approaches portrayed by rhizosphere microorganisms in enhancing plant health and resilience

Rhizosphere/host plant(s)	Associated microbe(s)	Functional attributes/mechanisms implicated	Potential implications on plants growth and fitness	References
Sugarcane	<i>B. subtilis</i> BS87 and <i>B. megaterium</i> BM89	Genes for trehalose metabolism, glycine betaine, PO, SOD, CSPs and phenazine (in <i>B. subtilis</i> BS87) Genes for chitinase, d-cysteine desulfhydrase and $\gamma$ -aminobutyric acid (in <i>B. megaterium</i> BM89)	ISR and bio-control measures Preferable candidate for bio-fertilizer Better plant growth performances and survival under harsh environment	Chandra et al. (2021)
Pigeon pea—maize intercropping system	<i>Enterobacter</i> sp. C1D, <i>Pseudomonas</i> sp. G22, and <i>Rhizobium</i> sp. IC3109	Chemotaxis and biofilm formation, root colonization, IAA synthesis	Plant growth promotion in mixed cropping system	Vora et al. (2021)
Basmati and non-basmati rice	<i>Enterobacter hormaechei</i> (AM122) and <i>Lysinibacillus xylanilyticus</i> (DB25)	Synthesis of 2-acetyl-1-pyrroline	Plant growth, aroma, and yield enhancement	Dhondge et al. (2021)
Wheat	<i>Pantoea</i> sp. MR1 and <i>Ochrobactrum</i> sp. SSR	Designed strains for dehydrogenase ( <i>gcd</i> ), phosphatase ( <i>pho</i> ) and phytase ( <i>phy</i> ), associated with P solubilization and mineralization	Improved root architecture and above-ground growth parameters P-solubilizing and mineralizing based microbial fertilizers	Rasula et al. (2021)
Juçara palm	Important bacterial genera <i>Pseudomonas</i> , <i>Stenotrophomonas</i> , <i>Burkholderia</i> , <i>Rhizobium</i> , and <i>Gluconobacter</i>	P solubilization (most common was <i>Burkholderia</i> genus), siderophore synthesis (genus <i>Pseudomonas</i> was the most frequent), auxins production	Enhanced nutrients acquisition and plant growth via hormonal modulation	Castilho et al. (2020)
Maize	<i>Bacillus</i> sp. MT7	Biofilm formation, rhizosphere competence, chemotactic behaviour, IAA production, P- solubilization and ammonia excretion	Bio-inoculants for tomato	Pathania et al. (2020)
Tomato	<i>Bacillus</i> spp.,	P and Zn solubilization, synthesis of IAA, phytase, siderophore, hydrogen cyanide (HCN), and ACC deaminase, biofilm formation and antagonism towards other microbes	Preferable candidate for bio-fertilizer and biological pesticide development	Kalam et al. (2020)
Mint	<i>Azospirillum brasilense</i> , <i>Azotobacter chroococcum</i>	Osmolyte accumulation, antioxidant activity, ABA	Microbial inoculants for moisture deficit stress alleviation	Asghari et al. (2020)
Potato, Rice, wheat, maize, soybean	<i>Serratia</i> spp.	IAA production, phytase production, AHLs,	As a nutrient enhancer and phyto-stimulater	Hanif et al. (2020)
False Flax	<i>Pseudomonas migulae</i>	ACC deaminase, phytohormone production, ABA as a stress hormone	Plant growth promotion and salt stress alleviator	Heydarian et al. (2018)
Wheat	<i>Pseudomonas tibansenis</i>	P-solubilization, IAA, siderophore, ammonia, ACC deaminase	Plant growth stimulation and drought stress alleviation	Kour et al. (2019)
Pigeon pea	<i>Pseudomonas</i> sp. NS 1 and <i>Bacillus</i> sp. NS 22	Antifungal metabolites, chitinolytic and other cell wall degrading enzymes (proteinase, cellulase, amylase, pectinase, lipase), siderophore, ammonia, cyanide, and ISR	Potential as biofungicides and biofertilizers to prevent <i>Fusarium udum</i> induced disease and promote plant growth	Dukare and Paul (2020)

Table 1 (continued)

Rhizosphere/host plant(s)	Associated microbe(s)	Functional attributes/mechanisms implicated	Potential implications on plants growth and fitness	References
Cucumber	<i>Bacillus amyloliquefaciens</i>	Secondary metabolites, phytohormones production, ISR,	Bio-control candidate for suppression of <i>Fusarium oxysporum</i> induced wilt disease	Liu et al. (2017)

compounds and volatile biocidal metabolites; (iii) synthesis of cell wall degrading enzymes, and (iv) indirectly by inducing systemic defenses in host plants (Dukare et al. 2020a).

Siderophore-producing rhizobacteria effectively compete with pathogenic fungi for limited Fe nutrients and make them inaccessible. This process results in pathogens inhibition via hindering fungal germination, metabolism, and virulence (Dukare et al. 2019). Several rhizosphere microorganisms produce many antimicrobial antibiotics (Dukare and Paul 2020). In producing bacteria, their biosynthesis occurs either from a ribosomal origin or by non-ribosomal peptides synthetases or polyketide synthases enzyme (Ramadan et al. 2016; Li et al. 2020). Most well recognized antifungal antibiotic substances include phenazine-1-carboxylic acid, DAPG, pyoluteorin, pyrrolnitrin, cepaciamide A, butyrolactones, subtilin, subtilisin, iturin, and surfactin (Goswami et al. 2016; Ramadan et al. 2016). Many microbial strains capable of controlling phytopathogens often harbor genes encoding antifungal antibiotics biosynthesis pathways. Using a transposon (Tn) mutant library, biocontrol genes and traits (swimming motility, siderophore biosynthesis, and other antifungal compounds) in *P. fluorescens* NBC275 (Pf275), a bacterial antagonist of pepper gray mold disease was revealed (Dutta et al. 2020). The genes encoding the chitin-binding protein (*gbpA*) and pyoverdine (*pvdI* and *pvdD*) biosynthesis remarkably contributed to their biocontrol potential (Dutta et al. 2020). The iturin is another important group of antifungal lipopeptides predominantly produced by certain *Bacillus* species. Iturin hampers pathogens growth by creating pores in the cell membrane and is followed by extensive leakage of cytoplasmic potassium ions. Among the iturin family, Iturin A has four open reading frames, *itu D*, *itu A*, *itu B*, and *itu C*. The expression products of the *itu D* gene play a crucial role in biocontrol activity (Ali et al. 2014). Besides, rhizobacterial originated metabolites such as hydrogen cyanide, ammonia, alcohols, sulfides, ketones, aldehydes cyclic lipopeptides, polyketides, and phenylpyrrole also show antifungal activity (Ramadan et al. 2016; Fouzia et al. 2015).

The latest advances in strain improvement techniques have made it possible to genetically alter the beneficial microorganisms to overproduce antibiotics and valuable bioactive compounds. In the recent past, an array of genomic engineering approaches, including precursor engineering, biosynthetic genes clusters (BGC) amplification, deletion of competing pathways, engineering of transcriptional/translational machinery, and manipulation of pathway-specific regulators have been developed for the bacterial strain improvement (Li et al. 2019). For instance, using the time-course transcriptome analysis, Li et al. (2018a) identified the chain of antibiotic-responsible promoters with a transcription profile under the optimal conditions. These responsive promoters can efficiently optimize the expression of native

actinorhodin (ACT) and heterogeneous oxytetracycline (OTC) BGCs in the bacterium *Streptomyces coelicolor*, leading to the substantial improvement in production titers of ACT (by 1.3 fold) and OTC (1.9 fold), compared with constitutive promoters (Li et al. 2018a, 2018b). Furthermore, different dynamic metabolic regulation techniques/approaches can effectively improve the production capacity of target compounds by balancing microbial growth and biosynthesis of specific metabolites (Li et al. 2019). Site-specific recombination (SSR) is another widely used technique for strain improvement, combinatorial biosynthesis, and heterologous expression of whole BGCs in numerous human and industrial bacterial species (Baltz 2012; Stark 2017; Merrick et al. 2018). In actinobacteria, SSR that are mainly derived from bacteriophage systems such as 8BT1, 8C31, and TG1 was used to develop cell factories through multi-copy amplification of BGCs or target genes (Baltz 2012). For instance, the antibiotic goadsporin was significantly increased (by 2.3-fold) by a gradual introduction of two additional copies of the 8C31 and TG1 integration systems based on goadsporin BGC (Haginaka et al. 2014). Finally, the advancements in genome sequencing, multi-omics, and genome editing tool are paving the way for enhanced production of targeted compounds in useful microbes.

Rhizobacteria producing extracellular hydrolytic enzymes (such as chitinase, glucanase, and cellulase) hampers pathogen growth by mycoparasitism (Dukare et al. 2020b). Bacterial chitinases belong to the glycosyl hydrolases family and possess the chitin-binding domain in carboxyl or amino-terminal (Hamid et al. 2013). The presence of the *chiA* gene encoding chitinase in *Serratia marcescens* and *Serratia plymuthica* are crucial in their ability to control plants diseases. Chitinase encoding genes (such as *ech42*, *nag1*, *chi33*, and *chi18-13*) allow attachment to fungal hyphae and cause mycoparasitism (Hamid et al. 2013). Similarly,  $\beta$ -1, 3-glucanase of *Paenibacillus* spp. and *Streptomyces* spp. inhibited the growth of *F. oxysporum*, whereas *Bacillus cepacia* adversely hampered the pathogenicity of *Sclerotium rolfsii* and *Rhizoctonia solani* (Compant et al. 2019). Root nodulating rhizobium can also act as a biocontrol agent of phytopathogens. For example, the pathogen suppression activity of *Rhizobium japonicum* against the soil-borne pathogens *Fusarium solani* and *Macrophomina phaseolina*, an etiological agents of soybean root rot was demonstrated (Al-Ani et al. 2012). Seed treatment with *R. japonicum* significantly improved germination and reduced soybean root rot index. Co-inoculation of rhizobia or AMF substantially reduced disease severity and incidence of red crown rot in soybean under low level of P condition (Gao et al. 2012). Furthermore, root exudates of soybean in the presence of inoculated rhizobia and AMF significantly hampered pathogen growth and reproduction. qRT-PCR studies revealed that the pathogen defense-related (PR) genes in roots, especially

*PR2*, *PR3*, *PR4*, and *PR10*, were overexpressed, leading to enhanced plant protection (Gao et al. 2012). In addition to direct mechanisms, certain volatile compounds produced by rhizobium are reported to suppress the invading bacterial pathogens of plants. As reported by López-Lara et al. (2018), the volatile metabolite methyl ketone 2-tridecanone (2-TDC) produced by rhizobium *S. meliloti* affected surface motility and biofilm formation in the bacteria. Furthermore, this chemical adversely obstructed several plant–bacteria associations (hampered alfalfa nodulation by rhizobia) and the incidence of tomato bacterial speck disease caused by *Pseudomonas syringae* (López-Lara et al. 2018). Genome sequencing studies have revealed the presence of several genes in rhizobia that are mainly contributing to its biocontrol potential. *Rhizobium* sp. strain 76 isolated from the rhizosphere of the wilt-causing agent *Fusarium oxysporum* f. sp. *cucumerinum* (Foc) migrated along with pathogen hyphal growth and reduced the disease incidence by 49%. The whole-genome sequencing analysis of this bacterium revealed several genes linked to biocontrol functions. The size of the whole genome was 5,375,961 bases, with two chromosomes and one plasmid and containing 5094 genes 76 (Sun et al. 2020).

### Quorum quenching mediated suppression of bacterial phytopathogens

Quorum quenching (QQ) causes degradation of the AHLs signaling molecules and monitors bacterial phytopathogen population density. QQ adversely affects the bacterial population's biofilm formation and virulence ability (Rehman and Leiknes 2018). The QQ involves the expression of QS signal degradation (*qsd*) operon encoding fatty acyl-CoA ligase QsdC and lactonase QsdA implicated in the degradation of acyl chain molecules and lactone ring (Barbey et al. 2018). The QQ is mediated via QQ enzymes and QS inhibiting molecules. The AHLs degrading many potato rhizospheric bacterial genera such as *Pseudomonas*, *Bacillus*, *Rhodococcus*, *Ochrobactrum*, and *Delftia* suppress bacterial pathogen, *Pectobacterium carotovorum* subsp. *carotovorum* mainly by degrading its lactone ring (Cirou et al. 2007). Furthermore, soil actinobacteria such as *Micromonospora*, *Streptomyces*, and *Rhodococcus* inhibit the AHL signal of *Chromobacterium violaceum* CV026 (Devaraj et al. 2017). Some bacteria can deactivate molecules related to the AHL family. Zhang et al. (2020a, b) reported that QQ bacterium *Acinetobacter* sp. XN-10 degraded AHL family molecules by dehydroxylation and hydrolysis. Subsequently, key intermediates produced compounds such as pentanoic acid, N-cyclohexylpropanamide, and methyl ester attenuated the pathogenicity of *P. carotovora* subsp. *carotovora* in carrot, Chinese cabbage, and potato. Some other cellular molecules can function as QQ compounds in bacteria. For example, the esterase

enzyme in rhizobacteria such as *Stenotrophomonas maltophilia* and *Pseudomonas aeruginosa* contributed to their QQ ability against solanaceous bacterial causing pathogen *Ralstonia solanacearum* (Achari and Ramesh 2018).

Certain bacteria such as *Lysobacter enzymogenes* LeM-omL have been genetically engineered to over-express QQ proteins to over-express QQ proteins, which subsequently reduced soft rot causing bacterial pathogen in carrot and Chinese cabbage (Wang et al. 2019). Similarly, potato and tobacco transformed with *Bacillus* gene *aiiA* encoding lactonases exhibited a superior tolerance to *Erwinia carotovora* (Dong et al. 2001). Similar to AHLs, DSF as a QS molecule in pathogens is deactivated by rhizobacteria. DSF degrading bacterium *Pseudomonas* sp. strain HS-18 carries genes such as *dig A*, *dig B*, *dig C*, and *dig D* that encode for fatty acyl-coenzyme A ligase. Expression of these genes in *Xanthomonas campestris* pv. *Campestris* diminished the surplus production of DSF molecules and thereby reduced its virulence. These showed that DSF-dependent gram-negative bacterial pathogens could be transformed as biocontrol agents via the insertion of the *dig* genes (Wang et al. 2020a, b).

### The suppression of plant-parasitic nematodes by rhizospheric microorganisms

Many strains of rhizobacteria are capable of inhibiting root invading plant-parasitic nematodes (PPNs) either through direct antagonism or altering feeding sites, killing vermiform stages, reducing their hatching and gall formation, and indirectly by priming host immunity (Elhady et al. 2018; Mhatre et al. 2019; Zhou et al. 2019; Topalović et al. 2020). The roles of the rhizosphere microbiome in suppressing PPNs have shown. For instance, maize and tomato rhizosphere inhabiting microbiome significantly hindered the reproduction and penetration ability of root-knot nematode (RKN), *Meloidogyne incognita*, and root-lesion nematode, *Pratylenchus penetrans* (Elhady et al. 2018). Developing a suppressive soil by enriching with the nematicidal and plant-useful rhizosphere microbiome may efficiently control PPNs infection (Zhou et al. 2019). Rhizobacteria, mainly *Pasteuria* spp., are among the most promising obligate parasites of many PPNs, are the most abundant microbes of nematode suppressive soils (Mhatre et al. 2020). *Pasteuria penetrans*, one of the predominant nematode parasitic bacteria, parasitized juveniles and killed almost 83% of the second-stage of RKN juveniles (Botelho et al. 2019). Further, certain strains of *Pseudomonas* and *Bacillus* native to suppressive soils parasitize eggs of PPNs. Kluepfel et al. (2002) studied the bacterium *Pseudomonas* sp. BG33R and identified five genes responsible for egg toxicity to the ectoparasitic nematode, *Mesocriconema xenoplax* infecting peach trees. Types of farming practices may alter the structural composition and

functional aspects of rhizosphere microorganisms regarding PPNs suppression. Accordingly, Harkes et al. (2020) demonstrated that microbial groups from taxa such as Burkholderiaceae, Enterobacteriaceae, and Pseudomonadaceae in the rhizosphere of organically grown *Pisum sativum* significantly reduced the population of RKN, *Meloidogyne chitwoodi* (Harkes et al. 2020). The soil bacterium *Klebsiella pneumonia* made soybean plants more immune against cyst nematode (*Heterodera glycines*) through regulation of ISR metabolic pathways related genes such as PR (PR1, PR2, and PR5) proteins and plant defensins (PDF1.2) (Liu et al. 2018). Khanna et al. (2019) demonstrated that some rhizobacteria could modulate defense pathways and metabolites in the host tomato plants. They reported that bacteria such as *Pseudomonas aeruginosa* and *Burkholderia gladioli* elicited ISR and suppressed RKN mainly due to the enhanced production of phenolic, osmoprotectants, organic acids, enzymatic, and non-enzymatic antioxidants. Some microbes may benefit the host by direct killing of PPNs and through priming host defense. For example, the bacterium, *Microbacterium* sp. efficiently reduces the root invasion of RKN *M. hapla* by firmly attaching to its cuticle (Topalović et al. 2020). Furthermore, this bacterium down-regulated all those defense suppressive genes triggered by PPN and activated defense systems, including ROS formation.

### Priming host plants immunity against invading pathogens

Indirectly, root and soil-associated microbe's prime host plants immunity by inducing systemic resistance (ISR). Numerous elicitors' molecules synthesized by microbe trigger ISR in the host plants via activating JA, SA, and ET signaling-dependent pathways (Pieterse et al. 2014; Tyagi et al. 2018). Several MAMPs such as flagellar proteins, chitin, LPSs, AHLs, cyclic lipopeptides, VOCs (e.g., 2,3-butanediol, acetoin), siderophore, and antibiotics are pivotal in activating ISR (Sharifi and Ryu 2018; Tyagi et al. 2018; Villena et al. 2018; Romera et al. 2019). Additionally, some specific compounds released in the root exudates trigger ISR in host plants. As studied by Stringlis et al. (2018), the antimicrobial compound, coumarin scopoletin, released by *A. thaliana* roots in the presence of *Pseudomonas simiae* primed host plants immunity against invading phytopathogens. Plants with ISR have improved physiological status, antioxidative profile, and defense system towards diverse plant pathogens.

*Pseudomonas* and *Bacillus* are the most well-known PGPR genera for inciting ISR. The bacterium *P. fluorescens* N21.4 elicit ISR in plants of *Rubus* sp. via activation of GAs dependent flavonoid and phenylpropanoids biosynthesis pathways (Garcia-Seco et al. 2015). Moreover, bacterium regulated gene expression and shaped the biosynthesis of



many secondary metabolites. Genes encoding enzymes that catalyze the conversion of phenylalanine to anthocyanins, catechins, and flavonols and coordinating the expression of flavonoid biosynthesis were identified in fruit (García-Seco et al. 2015). PGPR also modulates the expression profile of key regulatory genes involved in defense-related metabolic pathways and reactive oxygen species (ROS) production. The system biology analysis confirmed that bacterium *Paraburkholderia phytofirmans* PsJN primed innate immunity in *A. thaliana* against *Pseudomonas syringae* via triggering ET, JA, and SA based signaling pathways (Timmermann et al. 2019). Post 1 h of pathogen infection, bacterium regulated at least 48 transcription factors and a network with 4 clusters in *A. thaliana*. Within these clusters, *LHY*, *WRKY28*, *MYB31*, and *RRTF1* are the main transcription factors related to the activation of JA, ET, SA, and ROS pathways. In addition to direct antagonism, some rhizobacteria effectively inhibit pathogen activity via eliciting host resistance, as reported in bacteria *Pseudomonas aeruginosa* and *Bacillus stratosphericus* (Durairaj et al. 2017). These bacteria synthesized antibiotics and siderophores and depicted antagonistic activities against five different bacterial phytopathogens. Further, up-regulated expression of the defense-related genes (*PR-1a* and *PAL*) in tomato plants was noticed after the bacterial treatment (after 12 h). A deep RNA-sequencing analysis of host peanut plants in the presence of inoculated halotolerant PGPR, *Klebsiella* species (referred to MBE02), revealed that 979 genes were up-regulated, while 281 were down-regulated (Sharma et al. 2019). Most expressed genes were linked to phytohormone signaling, including JA, ET, and pathogen-defense signaling towards *Aspergillus* infection. In addition to priming host plants immunity, this strain directly inhibited the growth of many fungal pathogens, including *Aspergillus* (Sharma et al. 2019). The partial list of rhizosphere colonizing/beneficial microorganisms triggered some key genes of host plants implicated in their survivability and alleviation of challenged abiotic and biotic environmental conditions is given in Table 2.

## Recent advances and development in the area of beneficial PRM interactions

### Potential of “multi-omics” approach for elucidating rhizosphere microbiome functions

Due to the uncultivable nature of the rhizosphere microbiome, several culture-independent “omics” approaches such as metagenomics, transcriptomics, proteomics, metabolomics, phenomics, and interactomics are used for their in-depth analysis (Fig. 3) (Bell et al. 2014; Zhang et al. 2016). The metagenomics approaches reveal the rhizosphere

microbiome's vast structural and functional diversity (Melcher et al. 2014). Metatranscriptomics and metaproteomics provide insight into numerous genes translated and expressed in forming multiple PRM interactions in the rhizosphere and many other ecological niches (Von Bergen et al. 2013; Turner et al. 2013). Diverse metabolites formed in the cellular metabolism process are analyzed using the latest chemical analytical tools, chiefly liquid chromatography-mass spectrometry (LC-MS) and gas chromatography-mass spectrometry (GC-MS). Further, a nuclear magnetic resonance (NMR) tool deciphers the exact chemical structure of such metabolites and compounds secreted in the root exudation process (Zhang et al. 2012). Likewise, the exometabolomics tool can identify the metabolites utilization patterns of the rhizosphere microbiome (Baran et al. 2015; Swenson et al. 2018). Metabolomics and transcriptomics could help elucidate the precise functions of genes encoding biosynthesis of diverse signaling molecules implicated in different rhizosphere communication processes (Yan et al. 2017). Rhizosphere colonizing diverse microbial communities can be extensively analyzed using high-throughput or NGS. The 16S rRNA gene-based phylogeny strategy reveals the whole prokaryotic community, thereby knowing the evolutionary linkage and the microbial diversity (Ladoukakis et al. 2014). Using shotgun metagenome and 16S rRNA gene profiling, Bulgarelli et al. (2015) revealed the presence of structural and community diversity during various PRM and microbe-microbe associations in the wild and cultivated barley rhizosphere. Similarly, metagenomics combined with the 454-pyrosequencing technique unraveled the vast structural and functional diversity of the microbiome associated with the rhizosphere of *Avicennia marina* (Alzubaidy et al. 2015). The presence of a small “core” microbial consortium, mainly comprising of a symbiotic association of AMF with PGPR, probably acting as phytostimulatory bio inoculants in the rice cultivation, was demonstrated (Valverde et al. 2016). The metagenomics analysis confirmed the microbial diversity in the rhizosphere of red kidney beans (Suyal et al. 2015) and cultivated and wild rice varieties (Shenton et al. 2016). The obtained information on rhizodeposits and plant metabolites using these tools may widen our knowledge about the precise functions of metabolites in the beneficial PRM interactions in sustainable farming. Thus, understanding the biosynthesis and transportation of signaling molecules is achieved to optimize crop performance via regulating the rhizodeposition process (Jirschitzka et al. 2013).

The metatranscriptomics approach could collect information to identify the diverse metabolic pathways and active microbial community involved in the PRM interactions. The comparative metatranscriptomic technique revealed the taxonomic and functional attributes of wheat rhizomicrobiome in disease suppressive and non-suppressive soil (Hayden et al. 2018). *Stenotrophomonas* spp. and *Buttiauxella* spp. were

**Table 2** The partial list of rhizosphere colonizing/beneficial microorganisms triggered some key genes of host plants implicated in their survivability and alleviation of challenged environmental conditions

Rhizosphere colonizing/beneficial microorganisms	Activation/over expression of plants genes	Conferred benefits to host plants	Challenging conditions	References
<i>Bacillus</i> spp.	<i>RD20</i> , <i>RD26</i> , <i>DREB2</i> and <i>DREB1-2</i> (ABA-pathways dependent and independent stress-responsive genes)	Enhanced physiological, biochemical and antioxidative profile	Moisture deficiency	Bandeppa, et al. (2019)
<i>Bacillus amyloliquefaciens</i> SN 13	<i>GRAM</i> (lucosyltransferases, Rab-like GTPase activators and myotubularins)	Role in abiotic stress mitigation	Moisture deficiency and salinity	Tiwari, et al. (2021)
<i>Pseudomonas aeruginosa</i> strain Y1	Genes encoding for DETOXIFICATION-like proteins, aquaporins, autophagy-like, and <i>MAPKK2</i> -like <i>PR</i> genes: <i>MAMP-trigger immunity</i> (MTI), <i>RGA2</i> -like and <i>ETHYLENE-RESPONSIVE TRANSCRIPTION FACTOR 1B</i> (ERF1B)	Improved vegetative growth, glucosinolates, phenolic compounds, and lignin contents	Drought and pathogen-induced stress	Maulidah et al. (2021)
<i>Bacillus aryabhattai</i> ALT 29, <i>Arthrobacter woluwensis</i> ALT43	<i>GmFLD19</i> and <i>GmNARK</i> (Glycine max nodule autoregulation receptor kinase)	Enhanced stress responsive ABA content in NaCl stress	High salinity	Khan et al. (2021)
<i>Bacillus</i> sp.	Downregulated gene <i>OsNHX1</i> , Upregulated genes: <i>OsPIN1A</i> , <i>OsCATA</i> , and <i>OsAPX1</i>	Increased antioxidants level	Salt stress	Khan et al. (2021)
<i>Arthrobacter protophormiae</i> (SA3) and <i>Dietzia natronolimmaea</i> (STR1), <i>Bacillus subtilis</i> (LDR2)	<i>TaCTR1</i> and <i>TaDREB2</i> , encoding for a transcription factor	Improved tolerance to abiotic stress	Salt and drought condition	Barnawal et al. (2017)
<i>Pseudomonas putida</i> PS01	Up-regulation of <i>LOX2</i> Down-regulation of <i>APX2</i> and <i>GLY17</i>	Alleviated salt induced damages	Salt stress	Chu et al. (2019)
<i>Bacillus velezensis</i> 5113	<i>HSP26</i> and <i>HSP 17.8</i>	Mitigated the heat induced stress	Heat stress	Abd El-Daim et al. (2019)
<i>Bacillus cereus</i> (SA1)	Stress responsive transcription factor (SIHs-fAIa) and high affinity K-transporter ( <i>SIHAKT1</i> )	Ameliorated heat stress and significantly improved plant growth attributes	Heat stress	Khan et al. (2020)
<i>Enterobacter</i> sp. SA187	<i>H3K4me3</i> and modification of heat stress memory genes	Improved plant growth and thermo tolerance ability	Heat stress	Shekhawat et al. (2021)
<i>Bacillus</i> spp. <i>CJCL2</i>	Genes related to anti-oxidant enzymes <i>SodA</i> , <i>trx A</i> , <i>KatA</i> and <i>perR</i> genes <i>desR</i> , <i>desK</i> , <i>ResD</i> and <i>DegS</i> , <i>dpsU20</i> corresponding to stress response, osmotic stress regulation i.e., <i>ohrR</i> and <i>OpuAC</i> ABA response factor <i>ZmABF2</i>	Alleviated cold stress by enhancing metabolic and physiological functions	Cold stress	Zubair et al. (2019)
<i>Trichoderma harzianum</i> OMG16, <i>Bacillus atrophaeus</i>	ABA response factor <i>ZmABF2</i>	Adaptation to cold stress with increased growth parameters	Cold stress	Moradtalab et al. (2020)
<i>Pseudomonas aeruginosa</i> and <i>Burkholderia gladioli</i>	Metal resistance genes <i>CzcB</i> and <i>CzcC</i> , <i>CzcR</i> , <i>Pbr A</i> , <i>CadA2</i> and <i>ZntA</i>	Mitigation of Cd stress	Cadmium stress	Khanna et al. (2019)
<i>Bacillus cereus</i> NWUAB01	<i>cadA</i> , <i>CzcD</i> and <i>PbrA</i>	Confers metal resistance	Different metal stress	Ayangbenro and Babalola (2020)

Table 2 (continued)

Rhizosphere colonizing/beneficial microorganisms	Activation/over expression of plants genes	Conferred benefits to host plants	Challenging conditions	References
<i>Cellulosimicrobium funkii</i> AR6	Up-regulated genes: <i>LeEXP</i> (cell wall proliferation gene); <i>P5CS</i> , <i>DHN</i> , <i>HSP</i> and <i>MT</i> (stress marker genes) Dow-regulated genes: <i>NRAMP</i> (major metal transporter genes)	Improved plant growth, stress tolerance and reduced metal bioaccumulation	Chromium toxicity	Karthik et al. (2021)
<i>Trichoderma asperellum</i> GDFS1009 and <i>Bacillus amyloliquefaciens</i> 1841	Induction of <i>BLR-1/BLR-2</i> , <i>VELVET</i> , and NADPH oxidases genes	Enhanced plant growth and protection against plant pathogens	Plant pathogens	Karupiah et al. (2019)
<i>Bacillus velezensis</i> F21	Plant resistance genes <i>WRKY</i> , <i>MYB</i> , <i>bZIP</i> , <i>AP2</i> , and <i>NAC</i> .	Confers plant resistance against <i>Fusarium</i> wilt	Pathogen <i>Fusarium</i> sp.	Jiang et al. (2019)

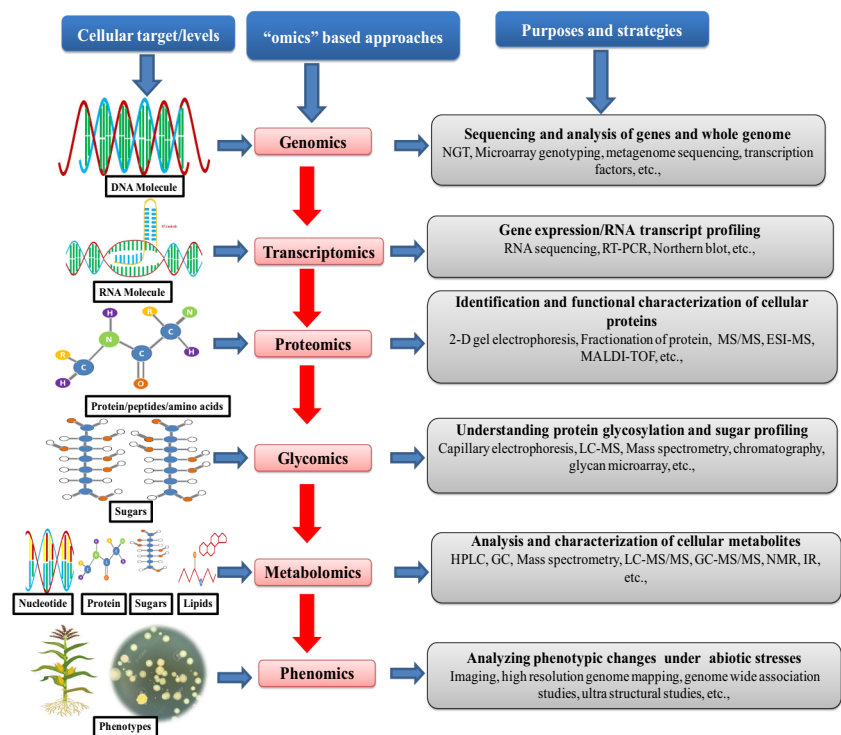
dominant in suppressive soil, while non-suppressive soil was predominated by *Arthrobacter* sp. and *Pseudomonas* spp. Further, the gene expression profile revealed the up-regulation of polyketide cyclase and several cold shock proteins (CSPs) genes in suppressive soil. In contrast, genes for antibiotic synthesis, transcriptional enhancer protein, ROS, and superoxide radicals were up-regulated in the non-suppressive soil. In brief, these tools can precisely show the microbial community assemblage and micro details of PRM interactions with various PGP attributes.

### Genome editing for customizing PRM interactions to improve plants growth and resilience

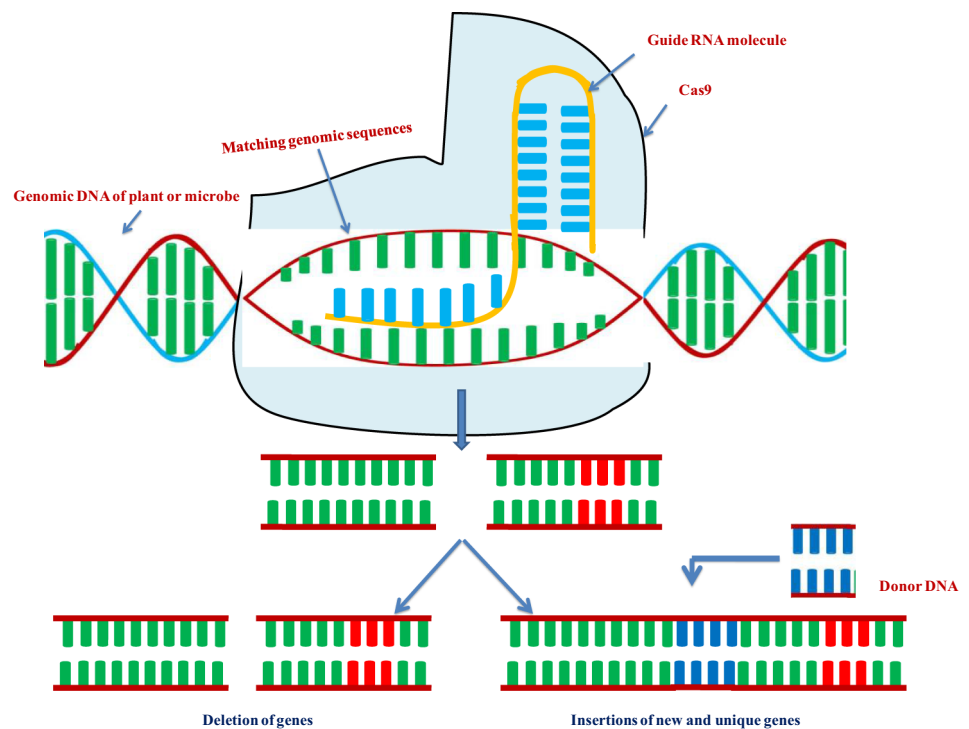
The application of CRISPR-Cas technology has enabled us to control the expression of genes using CRISPR interference (CRISPRi), having catalytically dCas9 and CRISPR stimulation (CRISPRa) systems (Parveen et al. 2020) (Fig. 4). The CRISPR-Cas system efficiently allows genome alteration with high specificity and accuracy, genes knock-down, and fluorescence imaging of RNA transcripts (Wang et al. 2020a, b). It has been established as a promising tool for strain improvement in bacteria. Many bacterial cells such as *Bacillus*, *Clostridium*, *Escherichia*, *Corynebacterium*, *Pseudomonas*, *Lactobacillus*, *Mycobacterium*, *Streptomyces*, etc. have been genetically altered for industrial product development (Cho et al. 2018; Fokum et al. 2019). Several metabolic pathways can be engineered for enhanced metabolite production by overexpressing or adding the desired genes (Fokum et al. 2019). Presently, this system has been more precisely *Escherichia coli* for producing many industrial biochemicals, biofuels, and other compounds with diverse applications (Parveen et al. 2020).

Under challenging environmental conditions, these techniques could decipher the decisive mechanisms in the plant-microbiome network, improving microbe-mediated plant growth, agronomic performance, phytoremediation, and developing disease-resistant cultivars (Shelake et al. 2019). Some of the potential applications of CRISPR-based GE techniques in the PRM interactions are (1) to uncover the gene functions in microbiome and plant (2) to fully knockdown the specific target genes (Bisht et al. 2019) and, (3) to obtain more precise and accurate genomic information and numerous gene functions at the molecular level (Shelake et al. 2019). At the rhizosphere microbiome level, the mutual interactions between legume root–rhizobia and pathogenic interaction of roots with *Pseudomonas syringae* have revealed the exact role and perspectives of responsible genetic factors (Glick 2014; Xin et al. 2018). This system has deciphered molecular facets of interactions of plant and rhizobacteria such as *Bacillus mycoides* EC18 and *B. subtilis* HS3 at the molecular level (Yi et al. 2018). In this system, the CRISPR/Cas9 mediated GE tool generated two mutants

**Fig. 3** Cellular targeted components, different purposes and strategies adopted in “multi-omics” based approaches in analyzing different aspects of PRM interactions



**Fig. 4** Schematic diagram depicting the working of clustered regulatory interspaced short palindromic repeats (CRISPR)-Cas mediated genome editing techniques



of *B. mycoides* EC18 and three mutants of *B. subtilis* HS3. By disrupting the *sfp* gene encoding 4'-phosphopantetheinyl transferase in *B. subtilis* HS3, authors demonstrated that the lipopeptide antibiotics (surfactin and fengycin) are essential for antifungal activity against *Rhizoctonia solani* and

*Fusarium culmorum*. Moreover, a green fluorescent protein (GFP)-tagged mutant approach revealed that the particular strain effectively colonized root hairs of grass (*Lolium perenne*) in a hydroponic system. Using CRISPR-Cas9 mediated genes (siderophore biosynthesis) interruption studies

in the bacterium *B. mycoides* EC18, the crucial role of siderophore (petrobactin) in plant growth support and root colonization was demonstrated (Yi et al. 2018). Further, the CRISPR-Cas system has been utilized for controlling pest and diseases of crops via targeted genes modifications in some microbial biocontrol agents such as *Beauveria bassiana*, *Purpureocillium lilacinum*, and *Trichoderma* species (Liu et al. 2015; Jiao et al. 2019; Chen et al. 2017) and host plants too. The CRISPR-Cas system may help speed up the microbiome-mediated phytoremediation process by customizing the xenobiotic degradation associated genes expression in plants and the specific microbiome (Mali et al. 2013). Several secondary metabolites (SMs) of plants and microbes are crucial in establishing a PRM network and communication. Hence, the CRISPR-mediated GE of SM biosynthesis pathway-related metabolic genes could allow its higher synthesis, discover novel aspects, and improve productivity (Shanmugam et al. 2019).

Such a tool has great potential in modifying rhizosphere processes by altering plant architecture and physiological status (Garcia and Kao-Kniffin 2018). For instance, the system may modify the root exudation process to recruit beneficial crop microbiota (Ahkami et al. 2017). Molecular breeding of legumes and non-legumes crops may facilitate the recruitment of more efficient N-fixing rhizobia, P-mineralizing, and other beneficial microbes in their rhizosphere. Briefly, these genome modification tools are imperative in unraveling the fundamental mechanisms and understanding how the host influences root microbiome diversity and their functionalities. Further, more detailed information obtained using the CRISPR/Cas9 could assist in devising the strategies for the precise selection of beneficial microbial groups in the rhizosphere.

### Nanotechnological interventions for improving the performance of microbial inoculants

Despite the established role of microbial inoculants in incrementing plant yield and productivity, their performance at the field level is often inconsistent and variable due to adverse and unfavorable environmental conditions (Gupta et al. 2015). Recent advances in nanomaterials can be used to augment the field efficiency of microbial bio inoculants by minimizing the detrimental effects on the environment. Nanotechnological science could play a pivotal role in transforming conventional farming into more precision-based agriculture (Subramanian and Tarafdar 2011). Various metal nanoparticles such as silver, gold, Cd, Cu, Zn, Fe, and Se, have applications in plant growth promotion, antimicrobial and antifungal effects, nano fertilizers, plant micronutrients, and plant disease control (Bahrulolum et al. 2021). Depending on the application required, nanomaterials are being used for their specific use in agriculture production. For example, in the suppression of

phytopathogens activity, antifungal properties of numerous nanoparticles such as like silver, Cu, zincite, nickel, and titania have been reported (De la Rosa-García et al. 2018). Likewise, metal oxide nanoparticles containing trace elements (such as Cu, Zn, and Fe) considerably contribute to plant growth and development (Wei et al. 2021). Before using nanoparticles in combination with the microbial inoculants, their antimicrobial effect and biocompatibility with the selected microbe need to be evaluated. For effective performance of the PGPRs, there requires to be a rational approach in providing a formulation and delivery of specific microbiome or their bioactive products in the field. Different nano-based recent approaches such as polymeric nanoparticle coatings, nano-formulations, and microencapsulated microbial formulations, referred to as nano-biofertilizers can efficiently deliver microbe inoculants (Vassilev et al. 2020). Nanobiofertilizer formulation comprising PGPR treated with different nanoparticles increment plant growth and prohibits pathogen proliferation and pathogenesis in the rhizosphere. Nano-formulations can help in the gradual and precise release of microbes/nutrients at the target sites. These mechanisms prevent the loss of nutrients from interacting with soil, water, and air, and other microorganisms in the ecosystem. Nanoparticle-based microbial nanoformulation is often provided with the nano-additives to (1) improve stability under a wide range of environmental conditions (e.g., desiccation, heat, drought, and UV exposure), (2) to offer substances required by the inoculums for growth and development, and (3) finally, to increase storage life and successful delivery of developed microbial products (Prasad et al. 2017; Jampilek and Králová 2017).

Upon the treatment of PGPR with titanium nanoparticles, PGPR was subsequently firmly attached to the rapeseed root surface and protected it from pathogen attack. Also, seeds of different monocots and dicot crops, pretreated with zinc oxide (ZnO) nanoparticles, increased the speed of seed germination (Mishra and Kumar 2009). In another recent study by Timusk et al. (2018), the novel use of nano titania nanoparticles combined with PGPR firmly attached wheat roots and successfully colonized seedlings. Nano-coated microbial formulation improved plant biomass and performance under diverse abiotic (drought and salt) and biotic (induced by pathogenic fungi *Fusarium culmorum*) stresses. Likewise, such a nano product may also successfully manage insect pests and weeds of crops. Therefore, nanoscience could assist in exploring the vast potential of beneficial microbial inoculants via facilitating their consistent and reproducible performance at the field level.

### Concluding remarks and future prospects

Here, we have focussed on the importance of a healthy microbiome for plants growth and development under challenging environmental conditions. Using the bilateral

**Table 3** Different areas of application, advantages, and limitations of “omic” based approaches

	Different areas of application	Advantages	Limitations
Genomics	Culture-dependent method for analyzing the microbial diversity and community structure in any environmental sample	Whole genome of organisms gives idea of antibiotic resistance, PGP traits and abiotic stress tolerant genes. Comprehensive information generation	Data management requires high skills, costly
Metagenomics	Culture-independent method for understanding the microbial diversity, population structure, and ecological functions of unculturable microorganisms in different ecosystem	Metagenome reveals novel genes, organisms, metabolic pathways. Gives diversity of uncultured organisms	Requires good knowledge of bioinformatics tools to analysis of data. No standardized and comprehensive pipeline for different aspects of metagenome analysis
Transcriptomics	To identify the patterns of gene expression in a microbial cell under wide array of biotic and abiotic stresses as well as during the PRM interaction	Provides direct insight into cell and tissue, specific gene expression feature	Requires good knowledge of molecular biology, use of computational tools
Proteomics	For revealing the regulation of biological systems by identifying key proteins as a signal of changes in physiological status of organisms For analyzing the structure and function of the proteins associated with the PRM interactions To unravel the metabolism, metabolic pathways, enzymes, and protein networking implicated in signal transduction system	Different approaches of proteomics involved, 2DE, DIGE, iTRAQ, Mass spectrometry which helps in separation of proteins, qualitative and quantitative expression of protein, high throughput. Generation of new hypothesis	Data processing and analysis is one of the major constraints
Metabolomics	To characterize the metabolites and their mechanisms involved in PRM interactions, plant growth development under abiotic stresses In combination with metagenomics, metabolomics can predict the functions of the genes	Reveals novel mechanism not previously reported/ identified. Successfully identified metabolic signatures, an unique tool to characterize the novel metabolite	Sensitive to various genetic and environmental stimuli

Note-Above information related to pros and cons of different “omic” based techniques was taken from Kumar et al. (2021), Manzoni et al. (2018), Teeling and Glöckner (2012), Chandramauli and Qian (2009) and Johnson and Gonzalez (2018)

“molecular dialogue” and biochemical and physiological aspects, we deciphered the several mechanisms implicated in the microbe incited plants growth, health, and stress resilience. The plant-linked microbiome is always fascinating and constantly expanding area of research throughout the globe. The potential of rhizosphere microorganisms to support plant health and fitness, especially under many adverse environmental conditions, is still not fully explored. Thus, more investigations using the latest scientific approaches are a prerequisite to elucidate the mechanisms of PRM interactions and the pathways of their reciprocal “molecular cross-talk” under a different set of suboptimal growth environments.

Herein, we narrated some contributing determinants allied with microbiome components and functional groups; yet, the causality of these associations demands further in-depth studies. Each biotic and abiotic stress must be dealt with within a specific context, examining distinct microbiomes, crops, and prevailing environmental conditions. Therefore, it is imperative to characterize a particular microbiome specific to various conditions, which further can maneuver the knowledge-based precise design of superior plant growth and health. Several PGPR isolated from challenging ecosystem have shown potential for developing promising inoculants to thrive in harsh soil conditions. Using the knowledge of niche-specific PGP traits of rhizobia, different inoculant combinations, and genomic manipulation approaches could augment the crop yield (Bellabarba et al. 2019). Beyond the pure metagenomic analyses to comprehensively interpretation of “multi-omics” findings, plants physiological and biochemical responses along with appropriate testing hypotheses and validations through in vitro and in vivo trials will be the next critical step. Every omics approach has pros and cons, which decide their application areas in the PRM interactions under abiotic stresses (Table 3). Further, a design of a system-based approach that combines genetics, biochemistry, physiology, immunity, and the defense biome is needed to gain insight into plant defense against biotic and abiotic stresses. A holistic understanding of the stress-induced microbiome shifts could facilitate the development of tailored “Defense Microbiomes” to fight crop stresses. Using such knowledge, new biotechnological products and innovative solutions that exploit plant-useful microbiome may be developed and introduced for improving agricultural productivity and environmental sustainability.

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and wrote relevant section in the manuscript. All authors read and approved the final manuscript.

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval and consent to participate** Not applicable.

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