Chapter

Potential Applications of Rhizobacteria as Eco-Friendly Biological Control, Plant Growth Promotion and Soil Metal Bioremediation

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Abstract

Modern agriculture has an immense problem in the depletion of agricultural productivity owing to a variety of biotic and abiotic stresses. Agriculture's sustainability and safety are dependent on ecologically friendly practices. Plant rhizobia have been proven to have an important role in disease control, as well as promoting plant growth, productivity, and biomass. Rhizobacteria are soil bacteria that live on the root surface and either directly or indirectly contribute to plant development. Rhizobia are used to induce mediated immune resistance through the manufacture of lytic enzymes, antibiotics, phytoalexins, phytohormone, metabolites. It supports the growth of plants through nitrogen fixation, nutrient enrichment, phosphate solubilization and phytohormone synthesis. In addition, it supports plants during different stresses such as temperature, osmotic, heavy metal and oxidative stress. Plant growth-promoting rhizobacteria have the ability to control heavy metal pollution of soils as well as enhancing plant growth in these soils. Efficient bioremediation is possible by using rhizobacterial inoculants, still, the distribution and functioning of microbes in the rhizosphere need to be fully explored. This review focuses on the effectiveness, biomonitoring processes and function in promoting plant development. Rhizobia application can be considered an alternative method for the improvement of biodiversity, agriculture, and the environment.

Keywords: rhizobia, biocontrol, antibiotic, plant growth promotion, heavy metal, bioremediation

1. Introduction

The productivity of crops is considerably impacted by nitrogen and phosphorous deficiencies, which are important for regulating the growth and development of crop plants [1]. To address this problem, it is important to carry out effective nitrogen management for sustainable agriculture. One of the interesting methods is to involve the use of microorganisms biologically fixing nitrogen which is utilized by the plant directly and is least susceptible to leaching and volatilization. Legumes establish a symbiotic interaction with the soil bacteria, termed Rhizobia, to fix atmospheric nitrogen. This helps in improving soil fertility, improving plant growth and prevents the necessity to use chemical fertilizers [2]. Besides this, agricultural productivity is significantly affected by the changing physical and biological properties of the soil [3]. In the past few years, the word "plant microsymbionts" has gained significant interest as plant microsymbionts directly affect the plant's performance and productivity. The plant microbiome comprises the complex adaptive gene pool, which originates from prokaryotic and eukaryotic organisms and even viruses, associated with the host's ecosystem [4]. Also, it has been well established that apart from changes in morphology, Bacteroides exhibit tremendous transcriptomic shifts and changes in biochemical processes especially in contrast to free-living bacteria [5]. There are various genetic and molecular pathways that govern the symbiotic compatibility, involving a wide variety of host and bacterial genes/signals with distinct adjuvants [6]. Consequently, understanding of the biological and molecular basis of symbiotic compatibility is essential in the development of tools for genetic modification of the host and/or bacteria to increase the efficiency of nitrogen fixation and to use it as a biocontrol agent. Here, in this review, we will address our latest summary of the microbial interactions, rhizobial efficacy, mechanisms as biocontrol, role in plant growth promotion, stress resistance and triggered immunity (ISR) against other microbes (pathogens). In fact, an insight into the genomes and recognition of candidate genes responsible for antibiotics, ISR and other metabolites from microbes is now possible. But the full range of molecular moieties involved in microbial interaction at an ecological scale deserves further study. Eventually, a definite and real improvement in the long term lies with the use of advanced analytical tools and their unification with classical experimental techniques to comprehend and then exploit soil–plant-microbe associations. Overall, it can help to improve biodiversity, agriculture and environmental studies further.

2. Microbial interactions

An existence of unseen host-microbial interaction has predominance from prehistoric times. While microbes are of minute size, they are available in nature in an astonishing majority, interacting directly or indirectly at different hierarchical levels of life. Almost all of these microorganisms are incredibly small, widely recognized by Archaea and Bacteria, although some microscopic forms include handful of fungi and even most protists. From an ecological standpoint, microorganisms are very often found in the soils as complex microbial population groups and have been investigated for several ties of microbiota-host interactions such as mutualists, endosymbionts, antagonists, parasites, and pathogens (**Figure 1**) [7].

Microbial community dynamic trends in the food chains look likely to be beneficial (positive), harmful (negative) or even sometimes neutral, with very little or no effect

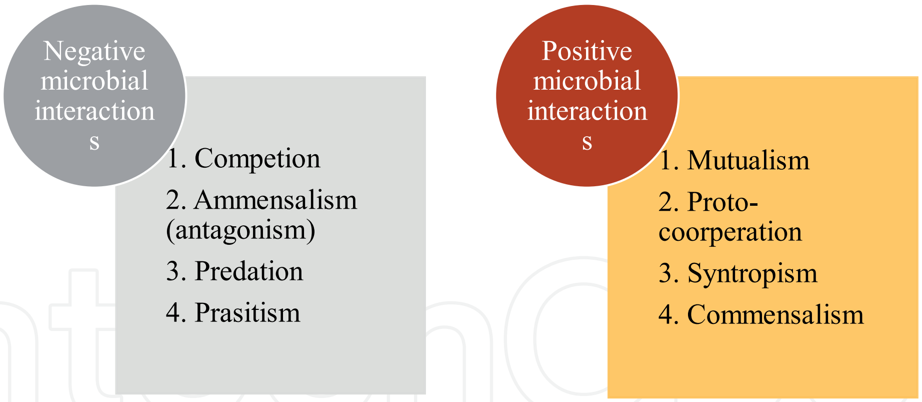

Figure 1.
Types of microbial interactions found in nature.

on their symbiotic associates [8]. Via physiochemical shifts, signaling mechanism-quorum sensing system (chemotaxis), cell transduction signaling through secondary metabolites, siderophores (used for iron acquisition) and gene expression microbial processes always have shown substantial impact on ecological parameters, resulting in established suitable alleles in diverse habitats [9]. Rapid and altered microorganism genetic variation corresponds both to biotic and abiotic sources of stress. Furthermore, atmospheric Nitrogen fixing microbial interaction and AMF symbiotic relationship activates a unique signaling process-CSSP (**C**ommon **S**ymbiosis **S**ignaling **P**athway) with calcium fluctuations in nucleus [10]. Many such strategies lead to an expansive population of microorganisms constantly getting established, culminating in pathogenic or beneficial effects on host plant species.

While many others have shown plants are able to select microbiota from all of diverse plant exudates including certain amino acids, carbohydrates and other biomolecules [11] which could also vary depending upon the plant itself, its stage of development and on biotic or abiotic conditions. Flavonoids, for example, are needed for talks between Legume-Rhizobia while AMF (mycorrhizal arbuscular fungi) rely solely on Strigolactone signaling [12]. In addition, the position of bacterial iron acquisition chelators that enforce a restricted supply of iron in the rhizospheric plane for pathogenic fungi constrains pathogen proliferation and occurrence. Consequently, synergetic microbial populations in the root micro-sites have a critical role to play in cloaking plants from disease deterioration, environmental factors and also ramping up nutrient uptake [13]. It has been well established that plant-associated microorganisms, particularly endophytic and rhizospheric microorganisms, can stimulate plant growth. A typical specified example is that of biotrophic symbioses between rhizobium and legume, such bacteria boost the growth of plant species by fastening atmospheric N_2, supplying of essential nutrients, enhance sequestration of minerals, produce phyto-hormones and also act as potential biocontrol against pathogens. Preliminary experiments on some endophytic and pathogen microbe genomes revealed pathogen degrade and displacement of host (host invasion), whereas the endophytic-mutualists express genes that aid in stress amelioration encoding proteins for nitrogen fixation and RubisCO [14]. During genetic interchange in a rhizobial symbiotic relationship, the root cortical cells are populated, making a distinction into nitrogen fixing bacteroids. Studies also show rhizobacter colonization into the root systems of non-leguminous plant species as such can be used as biocontrol in plant species other than legumes. Other popular, well-known, bacterial-based biocontrol method is *Agrobacterium* to prevent infection with *Agrobacterium tumefaciens.*In fact, myriad microorganisms (in particular belonging to genera *Bacillus, Pseudomonas* and *Trichoderma*) generate few chemicals against plant pathogenic fungi [8]. Bacterial isolates broadly find their application against plant pathogenic bacteria and fungi, whereas fungi are taken as biocontrols for pathogenic protozoans, pathogenic bacteria as well as pathogenic fungi. Juxtaposition between plants and several types of microbes has also been known to help mitigate many toxic metal build-up in plants [15]. While a general mechanism affecting mostly saprotrophs involves enhancement of microbial activity, selective different categories of symbionts can be stimulated in root microsites of plants. On the other hand, disease development by saproptrophs or biotrophs present in root micro-sites takes place only by developing antagonistic symbioses between pathogens and susceptible host plant roots. Importantly, the elimination of disease can sometimes be addressed through manipulating microbiological or physio-chemical surroundings mostly by classical practices- like use of soil refinements, agronomic rotational practices, fumigant use or even soil solarisation. A voluminous literature shows that interactive bacteria both symbiotic and pathogenic develop common signaling molecules to promote their host cell invasion through predominant substances such as conserved PAMP/MAMPs (Microbe-Associated Molecular Patterns) and protein effectors [16]. Organisms have developed recognizing mechanisms which differentiate between pathogens and symbionts and react in different ways to them, but this distinction often is not efficient; as a consequence, recognizing sensitivity also appears to occur both on pathogenic and symbiotic interaction [17, 18] at earlier stages. Thus, evidently microbial associations drive a complex sequence of interdependent metabolisms. In this paradigm of unexpected symbiotic partnership only host species utilize chemical synthesis capacities of symbiotic organisms to inhibit the development of certain environmental major competitors in order to sustain themselves [19]. In modern days, the philosophy of regulation of soil-borne diseases through the use of agro-chemicals such as pesticides and fungicides is now being modified through biological management [20]. Currently with the aid of molecular know-how, molecular pathways and processes involved in the interaction of microbes have been immensely explored.

3. Pathogen control mechanisms

Phytopathogens are those organisms which have the potential to adversely affect growth, development as well as the physiological activities of the crop. Any deviation in the environment which favors the proliferation of these phytopathogens result in a rapid outbreak of the diseases, leading to the crop destruction. Thus, reducing the yield and causing considerable loss of productivity. To prevent the development of disease it is necessary to control the pathogen mostly when their level is low. The organisms involved in biocontrol process are called as biocontrol agents and most of the biocontrol agents such as bacteria, fungi, algae, and nematodes which are found in root zone i.e., rhizosphere could influence various properties of soil and plants and thus act as defense mechanism against attack by pathogens [21]. It has been reported that there are some beneficial bacteria which can bring some changes in the rhizosphere as well as in the plants, leading to the enhancement in the plant growth, development and productivity and as such protect the plant from outbreak of various diseases [22]. Rhizobium being one of the categories of microorganisms which comprises of bacteria which can develop the symbiotic relationship with leguminous plants. Thus, are regarded as important nitrogen fixing organisms which play significant role in the maintenance of soil fertility [23]. However, many species of rhizobia are also reported to reduce the development of various disease-causing fungi, thereby increasing the yield of legume crops [24]. Several rhizobial strains such as *Rhizobium leguminosarum*, *Sinorhizobiummeliloti* and *Bradyrhizobium japonicum* have the ability to suppress soil-borne pathogens such as *Rhizoctonia solani, Pythium spp*., *Fusarium spp.,* and *Macrophominaphaseolina* in both legumes and non-legumes thus can be used as biocontrol against various soil-borne diseases [25]. Godebo et al. [26] suggested that *rhizobium* species can be used as biocontrol agents, since it inhibited the growth of aphanomyces in vitro in pea. *Rhizobia in combination with Tricoderma spp. can act as potential biocontrol agent* [27]. Colonization behavior of *Sinorhizobium meliloti* in the alfalfa rhizosphere reported to be useful for biocontrol. The application of *Pseudomonas maltophilia* in combination with *Mesorhizobium* and PSB was reported to be more beneficial as it showed the reduction in root rot incidence [28]. The study above shows that significant reports have been presented which favors the use of rhizobia as biocontrol agent against soil-borne pathogens, apart from being responsible for biological nitrogen fixation, thus acting as a befitting alternate measure over chemical treatments to control the spread of various plant diseases. Rhizobium is an effective biocontrol agent which helps in bringing down the growth of phytopathogens by implementing various mechanisms which include phytohormone production, siderophore production, production of antibiotics, HCN production, production of lytic enzymes, metabolite production and phytoalexin production and induction of systemic resistance [29].

3.1 Lytic enzyme production

Rhizobia produces several lytic enzymes which are responsible for degrading the cell wall of pathogens and as such are considered as an efficient source for biocontrol. Lytic enzymes produced by the rhizobia for biocontrol involves chitinases, cellulases, β-1,3-glucanase β-1,4-glucanase, β-1,6-glucanase, proteases, pectinase and amylases [30]. These enzymes are known to cause lysis of the fungal and bacterial cell walls and thus helps in controlling the population of plant pathogens [31]. Chitinase is a lytic enzyme which causes the lysis of pathogenic fungal cell wall through the disintegration of chitin in the cell wall of fungi and bacteria. This process involves the breakdown of glycosidic bond in chitin thus, reducing the chitin polymer into monomer. Endochitinase cleaves chitin randomly at internal points within the polymer of chitin and releases low molecular weight multimers and dimers. Exochitinase causes hydrolysis of chitin and releases di-acetylchitobiose with no monosaccharide or oligosaccharides formed. Protease is another lytic enzyme which prevents the protein of pathogen to effect plant cells as protease have the capacity to cause the breakdown of proteins of phytopathogens into smaller polypeptides or single amino acids. Some of the protease also involved in inactivation of extracellular enzymes of phytopathogenic fungi. Cellulases is another enzyme which causes the decomposition of cellulose. This reaction involves the hydrolysis of the 1, 4-β-D-glucosidic linkages in cellulose. The degradation of cellulose involves conversion of the cellulose into β-glucose which occurs by the combined action of important cellulolytic enzymes like cellulose / endoglucanases, exo-cellobiohydrolase/exo-glucanases and β-glucosidases. Cellulose is thereby converted into β-glucose by the synergetic act of all these cellulolytic enzymes. Glucanase are enzymes which causes hydrolysis of polysaccharide made of glucose subunits. This process involves two possible mechanisms viz., cleaving the glucose residues from the non-reducing end in sequence and breaking the linkages along the polysaccharide chain at random points and smaller oligosaccharides are released [32]. Among all these enzymes, chitinase are considered to be the most important ones as it acts as prime constituent of biocontrol and protect the plant against phytopathogens. It has been reported that rhizobial isolates producing chitinase results in inhibition of pathogenic microbes [24]. Damping-off of fava bean (*Vicia faba*) was reduced when rhizobium spp. capable of producing chitinase was applied as seed treatment either separately or along with mycorrhizal fungi [24]. Rhizobium strains isolated from *Sesbania sesban* has been reported to be produce chitinase. Rhizobium sp. Strain RS12, which have the ability to produce chitinase controlled the diseases of chickpea caused by *F. oxysporum*, *S. sclerotiorum* and *M. phaseolina* by reducing the growth and development of mycelia [33]. Plant diseases caused by several phytopathogens like *A. niger, F. solani, F. oxysporium, B. cinerea* and *R. solani* were reported to be controlled by chitinase from rhizobia, thus the latter was regarded as efficient biocontrol agent (34). Ability of rhizobia to produce lytic enzymes such as chitinase, β-1, 3 glucanase, protease, and lipase which bring about the lysis of pathogenic fungal and bacterial cell walls was also reported in various plants [3]. In fava (*V. faba*) bean infection caused by fungal mycelia of *F. solani* was reduced significantly by chitinase, protease and lipase [34].

3.1.1 Phytohormone production

Phytohormones or plant hormones are the organic compounds that cause the stimulation of plant growth and development at lower concentrations. They can be produced either naturally by plants in response to some specific stimuli or can be synthesized artificially and utilized for regulating the growth and development of plants [35]. Apart from regulating growth and development, these phytohormones also play an important role in biocontrol responses as they are involved in several synergetic processes between various plants and organisms. Therefore, these plant hormones not only helps in stimulation of plant growth, development, improvement in nutrient uptake, but also act as a shield against various biotic and abiotic stresses, and as such protection of plants from different phytopathogens [36]. Phytohormones include indole-3-acetic (IAA) acid (auxin), cytokinins, gibberellins and abscisic acid. Each of the plant hormones or plant growth regulators possesses specific functions.

a. **Auxin:** This is the phytohormone which is considered as an important hormone that helps in plant protection mostly in the form of indole acetic acid (IAA). It has been suggested that many rhizobia spp. can secrete plant hormones, such as auxin via indole acetic acid formation [37–41]. Tryptophan has been considered as the major precursor of IAA. However, rhizobium spp. can synthesize IAA even if the tryptophan is not present [42]. Soil-beneficial bacteria have the ability to synthesize IAA and are involved in many phyto-stimulations that could be beneficial in relation to the biocontrol. IAA is also reported to loosen the root walls to increase the secretion of various beneficial substance from roots, which can improve the bacterial growth in root zone [22]. Rhizobia producing IAA are reported to directly affect the growth of phytopathogens (44). Rhizobial IAA is able to affect pathogenesis as being involved in various physiological processes of plant like cell division, extension, rate of xylem development, formation of adventitious root and various pigments, photosynthesis, etc. Therefore, can act as an effector molecule in plant microbial interaction. More than 80% of nitrogen-fixing bacteria have reportedly resulted in the production of growth substances like indole acetic acid [43]. These substances enhance plant defense mechanism against various pathogens and improves the plant growth by increasing the total phenols, calcium content and polyphenol oxidase activity [44]. Rhizobial IAA was reported to have Phyto stimulation activity which resulted in suppression of more than 84% fungus mycelial growth of *S. rolfsii* because of the synergetic relation between in vitro bacterial IAA production and inhibition of *S. rolfsii* mycelial [45]. Treatment of nodules of vetch roots with *R. leguminosarum* bv. *Viciae* resulted in increase of IAA production by about 60 folds [46]. Application of *Pseudomonas* in combination with *Rhizobium galegae* causes increase in IAA production that results in increasing the number of nodules, nitrogen content, growth of shoot and root. However, biosynthesis of IAA was influenced by both environmental stress factors (acidic pH, osmatic stress, matrix stress and carbon limitation) as well as by genetic factors (auxin biosynthesis genes and the mode of expression. The bacterial strain *Mesorhizobium loti* MP6 produces indole acetic acid (IAA) under normal growth conditions inducing curling of root hair, inhibition of *Sclerotiniasclerotiorum* and improves the growth of Indian mustard (*Brassica campestris*) [29].

b. **Gibberellins:** Gibberellins are plant hormones (GA1-GA89) that regulates various plant developmental processes having significant function in stem elongation and leaf expansion. Gibberellins are involved in many aspects of plant physiology like, development of seedless fruits, flower and fruit maturation, breaking of seed dormancy, and sex expression. It has been suggested that rhizobium also have ability to synthesis gibberellins. Gibberellic acid possesses the ability of reducing the levels of reactive oxygen species (ROS) which results in improving the activity of antioxidant enzyme which further causes the progress in growth under adverse conditions [47]. Also, gibberellic acid applied exogenously was able to reduce effect of various stress like salt, oxidative and heat stress, on growth and germination in *Arabidopsis thaliana*, resulting in increased production of salicylic acid, which in turn increased the activity of isochorismate synthase 1. Rhizobium strains are also reported to produce cytokinins, which are involved in stimulation of cell division, development of root and formation of root hair. It was established that microbial cytokinins have the potential to act as biocontrol agents and can be used as a potent source against plant defense mechanism [48].

c. ***Abscisic acid:*** Abscisic acid is a naturally occurring phytohormone. It is a sesquiterpenoid which is being partly produced in the chloroplasts of plants and the biosynthesis occurs in the leaves. Abscisic acid is synthesized mostly during the stress conditions like moisture deficiency and low temperatures, heat and salinity. It is reported that *rhizobium* sp. can produce abscisic acid and stimulate various physiological processes of plants such as stomatal closure, inhibits the shoot growth, storage of protein in seeds during dormancy and is involved in causing proteinase inhibition by gene transcription, thus offers protection against pathogens.

d. **1-aminocyclopropane-1-carboxylic acid (ACC) deaminase:** Some of the rhizobia species like α and β rhizobia have the ability to produce enzyme ACC deaminase and the gene responsible for its production is *acdS*gene. ACC deaminase leads to the conversion of 1-aminocyclopropane-1-carboxylic acid

(ACC-precursor of ethylene) into α-ketobutyrate and ammonia. It has been reported that when rhizobia producing ACC deaminase are inoculated, the ethylene levels in the plant are reduced, resulting in increased nodulation, longer roots as well as improves rhizobial activity and thereby helps in bringing down various stress levels and also protects the plant from various pathogens (**Table 1**). The strains, which are reported to produce ACC deaminase involve *R. leguminosarum*. *Viciae*, *Rhizobium hedysari*, *Rhizobium japonicum*, *Rhizobium gallicum*, *B. japonicum*, *Bradyrhizobium elkani*, *M. loti* and *S. meliloti* [59].

3.1.2 Antibiotics

Biologicals are an effective way of combating pathogens in plants [60]. Antibiotics and other antipathogenic compounds may be secreted by beneficial rhizobacteria. Antibiotics are among the most important pathways for biocontrol [61]. Pathogens also acquire antibiotic resistance and other biological control mechanisms to prevent complete long-term control. A systematic strategy of numerous monitoring mechanisms is definitely safer than undue reliance on one solution while confronting pathogens. Pathogen-antagonistic bacteria can therefore adapt their mode of

Rhizobium ssp.	**Activity**	**Reference**
Mesorhizobium cicero	IAA production	[49]
Rhizobium leguminosarum	IAA production	[50]
R. leguminosarum	Cytokinin	[51]
Mesorhizobium sp.	IAA production	[52]
Bradyrhizobium sp.	IAA production	[40]
Rhizobium sp.(lentil)	IAA production	[39]
Rhizobium phaseoli	IAA production	[53]
Bradyrhizobium sp.	IAA production	[43]
Rhizobium sp.	IAA production	[54]
Rhizobium sp. (pea)	IAA production	[55]
R. leguminosarum	IAA production	[48]
Mesorhizobiumloti MP6	IAA production	[29]
ACC deaminase		
R. japonicum, B. elkani, M. loti, R. leguminosarum, Sinorhizobium spp.	Produce high level of ACC deaminase	[3]
R. leguminosarumbv. Trifolii SN10	Produces indole acetic acid and ACC deaminase which enhances rice growth	[56]
Lytic acid production		
Rhizobium strain	Produce enzyme: chitinases, b-1,3 glucanases, proteases and lipases	[3, 57]
Rhizobium spp.	Chitinases	[24, 58]
Rhizobium sp. strain RS12	Chitinases	[33]

Table 1.
Phytohormone production.

operation in the long-term to combat pathogens. In order to inhibit pathogens, PGPR produces antibiotics, such as lipopeptides, polyketides, and antifungal metabolites [62]. PGPR generates antibiotics that prohibit "saprophytic pathogens" from developing in the root zone; Combining strains that strengthen resistance to other antibiotics and biocontrol strains that modulate one or more antibiotics [61]. Rhizobia produces (TFX) tridolitoxin, an antibiotic narrow-spectrum peptide, and was found responsible for changes in microbial diversity in bean plant rhizosphere. Trifolitoxin (TFX) antibiotic by *R. Leguminosarum*bv. *Trifolii* T24 was documented for disease control. *B. Japonicum* produces rhizobiotoxin which protects Soya from *M. Phaseolina* [63]. *R. Leguminosarum* produces bacteriocins which have different assumed size characteristics (small, medium or large). *Trifolii* and *B. Japonicum* secrete antibiotics that could inhibit several phytopathogens have been documented [3].

3.1.3 Phytoalexins

Plants exist in dynamic ecosystems which are subject to frequent changes. They survive on a host of chemicals called secondary metabolites [64], which are essential for regulating secondary metabolism. Plants have a normal immune system to withstand biotic stress which can be activated by different agents. The plants have a unique potential condition called "priming" which is triggered in the plant before the pathogen challenge. The plants defensive mechanism against biotic stress involves the agglomeration of molecules (phyto-anticipins), which are converted to phytoalexins [65]. Phytoalexins are antimicrobial compounds generated by plants or some organisms as a response of the biotic and abiotic factors. These are "low molecular weight, anti-microbial" compounds synthesized after micro-organism or abiotic exposure in plants. Furthermore, elucidating the biosynthesis of different phytoalexins allowed the use of molecular biology methods to investigate genes encoding enzymes involved in their synthesis. This has led to new technologies to improve plant resistance. Phytoalexins show enormous diversity in various chemical groups, such as terpenoids, phenolics, steroid glycoalkaloids, compounds containing sulfur and indoles [66].

3.1.4 Induced systemic resistance

In addition to its role in N fixation, rhizobium serves as a tool for biocontrol of plant pathogens by triggering systemic resistance in plants. This is referred to as Induced Systemic Resistance [67]. The latter prepares the plant for defense against various phytopathogens [68]. The mechanism by which a non-exposed part of a plant imparts resistance to pathogenic microbes etc. by earlier exposure with the former is termed as induced resistance, thus it is triggered by an inducer that can be a biological or chemical agent. This induced resistance is not only activated at the site of pathogen attack but also at the parts that are very far from the site of induction so called induced systemic resistance (ISR) (**Figure 2**) and this ISR provides resistance to broad spectrum pathogens. Systemic resistance provided by ISR is regulated by signaling pathways in which different hormones are involved [69].

Rhizobial species inducing systemic resistance are *Pseudomonas*, *Bacillus, Trichoderma* and *Mycorrhiza*. Stringlis et al. [70] observed that these rhizobia are involved in the biosynthesis of antibiotics, flagella, siderophores and other volatile compounds which in turn stimulate microbe associated molecular pattern triggered immunity (MTI). A signaling pathway is generated in response to the perception of any of the above-mentioned substances. This is followed by another signaling

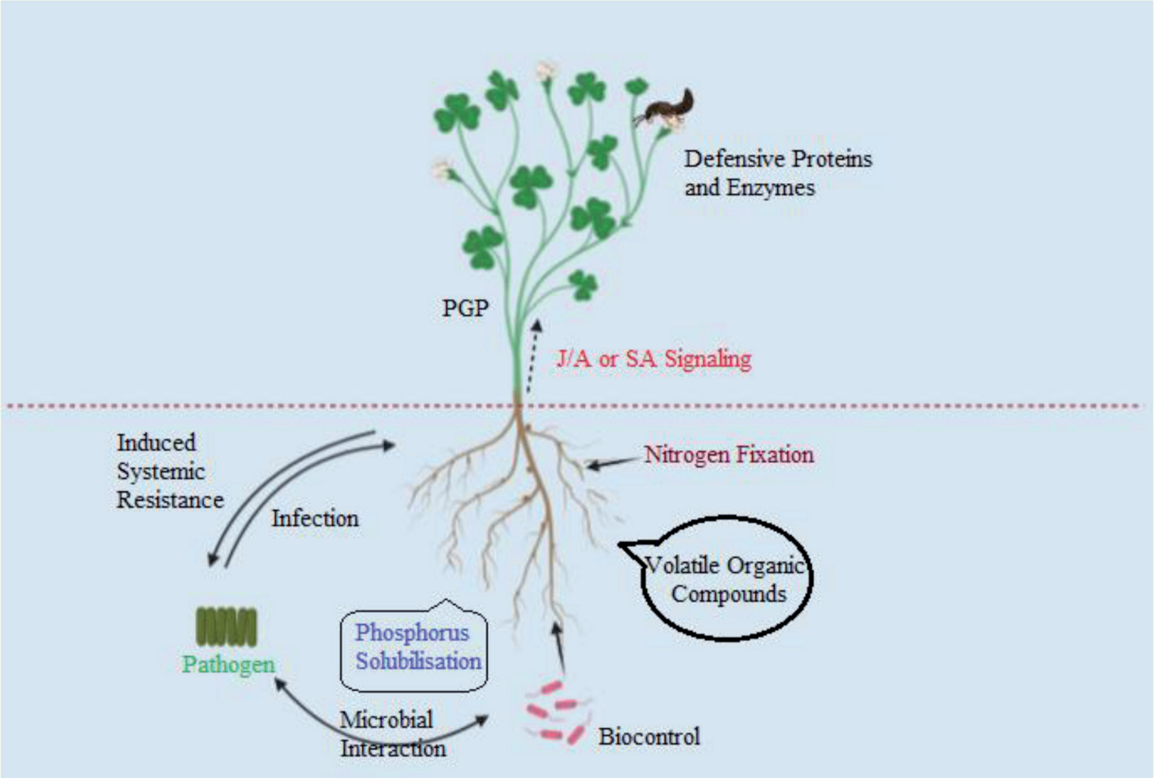

Figure 2.
Graphical representation of biologically induced disease resistance generated by beneficial microbes (ISR). It involves transport of long-distance signals in form of Jasmonic acid- salicylic acid (J/A & SA) and systemically circulate an improved defensive potential against a broad-spectrum pathogen in other plant parts and helps in plant growth promotion (PGP) as well.

pathway resulting in a systemic defense response [71]. Pattern-recognition receptors (PRRs) serve as sensors that have been evolved to differentiate and recognize bacterial and fungal products called pathogen associated molecular patterns (PAMPS). Moreover, in case of the damage/invasion caused by the pathogen attack an endogenous signal is produced. The ISR imitation in plants requires microbes that can be beneficial as well as able to effectively colonize the plants root system [72]. Recently microbial aspects around the root micro-sites harboring bacteria and fungi slowly gained interest because of their potential to trigger resistance (induced systemic resistance ISR in case of bacteria/systemic resistance in case of other microbes) in plants as a measure of biocontrol [17]. For instance, 22 kDa xylanase isolate of fungal endophyte *Trichoderma* when introduced into the plant cells evokes the plant's defensive response including potassium, hydrogen ions, calcium ion movements, PR protein synthesis, ethylene formation, glycosylation of phytosterols and fatty acid acylation [17]. Among the prominent changes taking place during ISR are:

1. Strength and stiffness in an epidermal and cortical plant cell wall.

2. Relocation of recently created barriers / blocks of impermeable lignin, callose and phenolic compounds away from an affected/entry site.

Plant responds to a number of biochemical signals induced by soil and plant-associated microbes. The strength and stability of its cross-talk signal play key role in determining the quality of resistance against pathogens. The interactions with these microbes can be in the form of different relationship possibilities (symbiosis, mutualism competition, predation, commensalism, etc. and host. At the initial stage, hypersensitive response gets active, a mechanism used by plants to prevent the spread of local infection by microbial pathogens [73]. While as for a positive mutual association both the host and the microbe must have to respond to the signals equally so that there is mutual benefit for both. In the association between the rhizobium and mycorrhiza, it has been studied that the host secretes strigolactones and flavonoids. Strigolactones are a class of plant hormones which are responsible for stimulation of branching and growth of mycorrhizal fungi. These strigolactones and flavonoids are also responsible for activation and production of symbiosis (sym) and Nodulaton (Nod) factors by microbes. The manipulated entry of rhizobium systematically triggers the whole downstream molecular defense system [67]. Which in turn builds a successful symbiotic relationship by activating common signaling pathways. By modifying the transcriptional programing many free-living plant growths promoting rhizobacteria (PGPR) positively respond to the root exudates that are involved in chemotaxis, energy metabolism etc. [74]. The mode of action of ISR is priming for enhanced defense, it does not cause direct activation of systemic resistance. Elevated transcript levels of various transcription factors were found in *Arabidopsis*eg. AP2/ERF were highly expressed. Among these several members are involved in regulation of jasmonic acid (JA) and ethylene (ET) defensive pathways. ISR by soilborne microbes is mostly regulated by JA/ET pathway. In the rhizosphere ISR is responsible for microbial antagonism, any host pathogen interaction enriches the microbiome and thus provides protection against diseases. The production of elicitors by beneficial microbes is also required in order to result in the onset of systemic immunity [69] so that there is a balance between the costs and benefits of mutualism. Plant-growth-promoting rhizobacteria (PGPR) were successful in managing complex diseases such as anthracnose (*Colletotrichum spp.*), angular leaf spot and bacterial wilt (*Erwinia tracheiphila*). Oxidative changes were observed in soyabean roots after inoculation with *Bradyrhizobium japonicum* [75]. With advancement of next generation sequencing technologies, it has been very easy to study the vast microbial diversity in the rhizosphere. Earlier studies have shown that there are different subsets of diversity in soil bulk, thus type of soil is an important factor for determining rhizosphere microbial community.

4. Mechanism in plant growth promotion

Modern agriculture is experiencing a number of challenges *viz*., poor soil fertility, serious pathogen and pest attacks, climate changes. Agricultural production must be sustainable and at the same time eco-friendly. This could be achieved by using environmentally sound approaches such as use of bio-fertilizers, bio-pesticides and by returning the crop residues to the soil thereby increasing the organic matter content of the soil. Application of crop residues to the soil resulted in increased yields compared to control [76]. Microbial inoculants which have been used for centuries, is a safer and relatively cheaper tool for promoting plant growth and improving soil health properties by different mechanisms [22]. Nitrogen fixing rhizobium bacteria live in association with legumes, infect them and form nodules in its roots. In case of non-legume crops they interact asymbiotically [77]. They are found in the rhizosphere to make use of the nutrients as the latter has plentiful nutrients oozed from roots of plants. They either have a direct or indirect control over plant growth, by synthesizing phytohormones, control pathogen infestation by influencing the production of several enzymes like cellulase, protease, lipase and other such productions thereby inducing whole plant resistance against pests or by soil nutrient enrichment through their nitrogen fixation and phosphate solubilizing ability. Microbial inoculants have multiple beneficial effects, particularly as plant growth promoters (PGP). Not only this but PGPR also help in combating a variety of abiotic stresses like temperature stress, salinity as well as drought stress, heavy metal toxicity and other types of abiotic stresses [3]. According to their closeness and interaction with the plant roots Rhizospheric bacteria have been classified as: (1) rhizosphere occupying bacteria (2) bacteria's forming colonies at the surface of roots (3) bacteria's living inside the roots (endophytes); and (4) bacteria's residing in the cells of root nodules. Bacteria's that belong to these groups are known as plant growth promoting rhizobacteria (PGPR) [78]. The bacteria belonging to 1 to 3 categories as extracellular PGPR (ePGPR) while the 4th category was named as intracellular PGPR (iPGPR). The ePGR includes following genera: *Bacillus*, *Pseudomonas*, *Erwinia*, *Caulobacter*, *Serratia*, *Arthrobacter*, *Micrococcus*, *Flavobacterium*, *Chromobacterium*, *Agrobacterium*, and *Hyphomicrobium* whereas *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium* and *Allorhizobium* belong to iPGR category. To strengthen the use of soil rhizobia for the attainment of sustainable and eco-friendly production methods a basic understanding of their functioning and means by which they facilitate plant growth is needed.

4.1 Plant growth promotion by direct mechanisms

4.1.1 Nutrient enrichment by Nitrogen fixation

Nitrogen is a macronutrient required by the plants for synthesizing proteins, nucleic acids and enzymes. Plants synthesize their food with the help of chlorophyll and nitrogen forms an essential component of chlorophyll. Despite the fact that the atmospheric air comprises of about 78% of nitrogen N, this gas is not available for use by the plants directly. Nitrogen application to crops has led to an enormous increase in food production which has eventually resulted in increased human population. Haber-Bosch process being the source of industrial nitrogen fertilizers, has been regarded as the primary cause of explosive growth in human population [79]. Currently, large amounts of synthetic chemical fertilizers are being used in agriculture and these fertilizers have been used beyond their limits, moreover they are expensive and polluting. Application of chemical fertilizers liberates reactive nitrogen into the atmosphere which leads to emission of green-house gases and at the same time eutrophication of water bodies. The detrimental effects of fertilizer use become much more pronounced when these are applied injudiciously. The economic and most importantly environmental concerns make the use safer and relatively cheaper alternatives necessary. Biological nitrogen fixation, whether symbiotic or non-symbiotic is a potential alternative promoting plant growth and hence increasing production [80]. Plant growth promoting-rhizobia are able to perform biological nitrogen fixation (BNF) and thus help plants in nitrogen assimilation. They live in soil and after producing specialized structures (nodules) in legumes by infecting their roots, they fix the atmospheric nitrogen (N_2) and convert the same into a more readily useable form i.e., ammonia (NH_3) so that the plants can utilize it for their growth. These rhizobia in turn get organic acids which serves as a source of carbon and energy. Two classes of genes: 1. Nodulation (nod) genes and 2. nitrogen fixation (nif) genes are needed

Function of the gene	Gene
Nodulation genes	
nodA	Acyltransferase
nodB	Chitooligosaccharide deacetylase
NodC	N-acetylglucosaminyltransferase
Nod	Transcriptional regulator of common nod genes
nodIJ	Nod factors transport
nodPQ	synthesis of Nod factors substituents
nodX	Synthesis of Nod factors substituents
nofEF	Synthesis of Nod factors substituents
Other nod genes	Several functions in synthesis of Nod factors
nol genes	Several Functions in synthesis of Nod factors substituents and secretion
NOE genes	Synthesis of Nod factors substituents
Nitrogen fixing genes	
nifHDK	Nitrogenase
NifA	Transcriptional regulator
nifBEN	Biosynthesis of the Fe-Mo cofactor
fixABCX	Electron transport chain to nitrogenase
fixNOPQ	Cytochrome oxidase
fixLJ	Transcriptional regulators
fixK	Transcriptional regulators
fixGHIS	Copper uptake and metabolism
fdxN	Ferredoxin

Table 2.
Genes involved in nitrogen fixation.

for the establishment of a good association between rhizobia and plants. Bacterial genes present in plasmids, code for Nod and Nif proteins [81]. Mainly three nod genes namely nodC, nodB and nodA are involved in nitrogen fixation. In addition to this, other nod genes viz., nod, nol or noe have been found in some rhizobial species [82]. Nodulation genes code for the enzymes involved in production of nodulation factors (nod) [77]. The roots of leguminous plants produce flavonoids in the rootzone, these compounds stimulate the expression of nod genes in the bacteria. Their expression in turn produces the Nod factor, which is a lipochito-ologosachharidic nodulation signal. This signal triggers mitosis and nodule formation [83]. Nitrogen fixation genes include genes for nitrogenase. Nitrogenase forms the most important part of BNF. The enzyme has 2 components: a. dinitrogenase reductase and b. dinitrogenase. The former gives electrons to the later which reduces N2 to NH3. BNF involves different clusters of genes for nitrogen fixation and nodule formation in leguminous plants (**Table 2**) [77].

4.1.2 Phosphate solubilization

Phosphorus is another macronutrient essential for proper development of plants. Its deficiency can adversely affect plant growth. After nitrogen phosphorous is the most limiting nutrient for plant growth [84]. Phosphorus forms an integral part of DNA and RNA, enzymes and phospholipids. Besides this, important processes like photosynthesis, formation of roots, flowers, ability of plants to cope up with diseases depend on the optimal levels of phosphorus [85, 86]. Although the soils are naturally rich in phosphorous reserves but the amount that is available to plants for their use is only a small fraction of the original amount present. This is because phosphorus is predominantly present in insoluble forms in soil and plants can only make use of phosphorus in soluble form i.e., the monobasic (H_2PO_4 -) and dibasic forms ($H_2PO_4{}^{2-}$). Phosphorus availability is governed by various factors such as pH of soil, soil temperature, amount of organic matter present in the soil, root system and most importantly soil microorganisms. The latter has a critical role in increasing P availability to plants. Soil P concentration ranges between 0.01-3 mg P $L^{-}1$ which is very small compared to the amount that plants need for normal growth. Therefore, to make sure that the plants are not devoid of P, remaining amount is compensated by soil rhizobia using their phosphate solubilizing property. These rhizobia are referred to as phosphate solubilizing microbes (PSMs), having the ability to hydrolyze insoluble phosphorus in soil into readily soluble form. They develop a network in the rhizosphere around the plant roots, allowing them to absorb P from a broader area. The use of PSMs is an environmentally safe and cheap method to reduce the insufficiency of phosphorous and promote its absorption and assimilation by plants. PSMs are able to convert the insoluble phosphorus into soluble form by lowering the pH, chelating cations and mineralization [84]. Application of phosphate solubilizing bacteria belonging to following genera*: Achromobacter, Agrobacterium, Bacillus, Pseudomonas, Erwinia, Flavobacterium, Microbacterium and Rhizobium* has resulted in increased phosphorus uptake and eventually higher yields.

4.1.3 Potassium solubilization

A diverse range of soil microorganisms such as saprophytic bacteria, fungi, and actinomycetes show potential to solubilize potassium effectively converting soil K to plant-available forms [87–90]. Among these, solubilizing bacteria (KSB) can dissolve K-rich materials and convert insoluble K to soluble forms that plants can absorb. Although some KSB can work anaerobically, the majority of these are aerobic. The potassium solubilizing rhizobacteria (KSR) use a number of ways to make the K available to plants. Mechanisms such as Acidolysis, chelation, exchange reactions, complexolysis, and the production of organic acids are few well known alternatives. The acidolysis (organic and inorganic acids, as well as the synthesis of protons) is the main mechanism of K mineral solubilization [87, 91–95]. Formation of organic acids by KSB that are useful in releasing K from K-bearing minerals include oxalic acid, tartaric acids, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, lactic acid, propionic acid, glycolic acid, malonic acid and fumaric acid [96–103]. Tartaric acid, citric acid, succinic acid, ketogluconic acid, and oxalic acid are the most effective acids secreted by KSB among the several organic acids involved in the solubilization of insoluble K. *Acidothiobacillus ferrooxidans, Paenibacillus spp., Bacillus mucilaginosus, Bacillus edaphicus,* and *Bacillus circulans* are among the bacteria that can solubilize K minerals such as biotite, feldspar, illite, muscovite, orthoclase, and mica [96, 104]. It has been observed that *B. mucilaginosus, B. circulanscan, B. edaphicus, Burkholderia, A. ferrooxidans, Arthrobacter sp., Enterobacter hormaechei, Paenibacillus mucilaginosus, Paenibacillus frequentans, Cladosporium, Aminobacter, Sphingomonas, Burkholderia, and Paenibacillus glucanolyticus* solubilize K from silicate rocks. Further, *B. mucilaginosus, B. edaphicus,* and *B. circulanscan* have been identified as excellent K solubilizers in soil bacterial populations [88, 89]. Furthermore, microbial degradation of organic materials produces ammonia and hydrogen sulphide, both of which can be oxidized in the soil to make powerful acids like nitric acid (HNO_3) and sulfuric acid (H_2SO_4). Consequently, K+, Mg$_2$+, Ca$_2$+, and Mn$_2$+ are displaced from the cation-exchange complex in soil by hydrogen ions [105]. Organic acids produced by KSB can liberate K ions from the K mineral via complexing agent Si$_4$+, Al$_3$+, Fe$_2$+, and Ca$_2$+ ions (chelating) linked with K minerals, additional to decreasing soil pH [106, 107]. In addition, accumulation of diverse extracellular polymers (mainly proteins and polysaccharides) has also been linked to the release of K from K-bearing minerals [99, 103, 108]. Such substances act as adhesive structures to the surface of minerals or rocks. Fresh microbial EPS (exopolysaccharides) solution, for example, accelerates the dissolution rate of feldspars by forming complexes with framework ions in solution (Welch and Vandevivere 1994). Other PGPRs (for example, IAA-producing bacteria) may also play a role in delivering K to plants via boosting root exudates [109].

Under greenhouse and field circumstances, studies have demonstrated that inoculating seeds and seedlings of many plants with KSB improves germination percentage, seedling vigor, plant development, yield, and K uptake [87, 88, 110–115]. Several studies show that KSB inoculation improves the growth of a variety of crops [101, 103, 112, 116–125]. Overall, studies indicate application of KSB as bio-fertilizers for agriculture development can reduce the usage of agrochemicals while also promoting sustainable crop production

4.1.4 ACC deaminase production

The infection caused in the roots by rhizobium bacteria during nodule formation results in stress conditions. Consequently ethylene, a stress regulating hormone, inhibits the infection put forth by the bacteria, besides restricting nodulation and root growth [126]. Specific genes are involved in the interaction mechanisms of Rhizopheric bacteria with the plants by means of which they influence their growth. One of these genes encoding for the enzyme ACC deaminase, is involved in cleaving ACC, the precursor of ethylene biosynthesis produced by plants. ACC deaminase degrades ACC into ammonium and ketobutyrate and prevents ethylene biosynthesis [127]. Under limited ethylene concentration, rhizobial colonization of the roots is enhanced which result in the formation of a greater number of nodules on the host plant. Horizontal Gene transfer allows the spread of acdS within the species [128]. However, the genetic analysis carried out by Nascimento et al. [129] revealed that acdS are inherited vertically during evolution. Glick, [22], confirmed that the bacteria which produce IAA synthesize high level of ACC deaminase which inhibits ethylene biosynthesis and promote plant growth, root nodulation and increase uptake of minerals from the soil. Rhizobial strains including *R.leguminosarum, R. hedysari, R. gallicum, B. elkani and S. meliloti* have been reported to synthesize ACC deaminase [3].

4.2 Plant growth promotion by indirect promotions

4.2.1 Salt stress and osmotic stress

Plant growth improvement has been of great concern since the beginning of agriculture. There are various abiotic factors including temperature, pH, heavy metal toxicity, salt stress which obstruct plant growth and crop productivity [130]. Among them salinity stress is a real hazard for plant growth and production. Under saline conditions plants uptake high amounts of salt which interferes with their physiological and metabolic processes which hampers their growth and makes their survival difficult. Reclamation of saline soils by conventional methods i.e., adding soil amendments like gypsum, calcium etc. do not help to overcome salinity stress completely, moreover they adversely affect the ecosystem. Therefore, for the enhancement of plant growth and productivity, development of sustainable and safer methods is of utmost importance [131]. Large number of microbes belonging to different genera of salt tolerant plant growth promoting rhizobacteria (ST-PGPR), present in the soil are able to tolerate salinity stress as well as promote plant growth [132]. These rhizobacteria (ST-PGPR) include genera *Pseudomonas, Enterobacter, Agrobacterium, Streptomyces, Bacillus, Klebiella* and *Ochromobacter* [133, 134]. Salt-tolerant rhizobium isolated from legumes growing in sand dune sand tree legume [135] were able to tolerate upto 2.5–3% of NaCl concentration. In 2018, Zhang et al. [136] isolated 305 bacterial strains and found that 162 out of 305 could grow in NaCl concentration of 150 g/l. For boosting nitrogen fixation and productivity in high salt containing soils co-inoculation of legumes with salt tolerant rhizobial bacteria is a sustainable solution. Under non saline and saline condition silicon was found to enhance growth and nitrogen fixation in leguminous plants [137].

4.2.2 Temperature stress

Worldwide climate change had led to an increase in temperature, which adversely effects plant growth and development. Elevated temperatures result in decreased rate of photosynthesis, negatively influence plant water relations, flower and fruit development. Soil rhizobia indirectly help plants to combat heat stress. Most rhizobia prefer an optimum temperature range of 25–30°C for their growth, however, during their life cycle they experience a temperature out of this range. The growth promotion effect of different PGPR strains in plants was attributed to their nitrogen fixing ability but these effects were noticed prior to the beginning of nitrogen fixation [138]. This shows that the favorable effects of rhizobium in alleviating temperature stress does not depend on nitrogen status. It is due to stimulation of genes to express under high temperature stress conditions. The expression of these genes is regulated by heat stress transcription factors (Hsfs) [139]. HSPs are a family of proteins that are induced by a sudden temperature rise, they include chaperones and proteases, which confer high temperature tolerance to bacteria and thus contribute to the tolerance mechanism [140]. A microarray study conducted in *Sinorhizobiummeliloti* showed that 169 genes, which included the genes coding for HSPs and chaperones, were up regulated under high temperature conditions. Chaperones, like DnaK–DnaJ and GroEL–GroES, form an important component of the heat shock response. After heat shock, the hydrophobic domains of proteins are exposed, and they get denatured. These chaperons help the denatured proteins to get back to their original conformation [141]. The increased expression of chaperone genes was induced in heat tolerant strains compared to the strains of the same species that were sensitive to heat. Under high temperature stress HSPs increase the stability of cell membrane, thereby conferring heat tolerance to both, rhizobacteria as well as the plant under stress. Breeding of heat tolerant or development of transgenic heat tolerant cultivars is a laborious and less economic method. Hence, the application of rhizobacterial inoculants to plants under temperature stress should be preferred as it is relatively cheaper and less time consuming. Various physiological and biochemical changes in plants, are induced by low temperature resulting in poor plant growth and low crop survival rates [142].

Rigidification of membranes due to the decreased fluidity of cell membrane is one of these changes that plants experience when exposed to chilling stress [143]. Response to cold shock results in the synthesis of cold shock proteins (CSPs). Rhizobia strains isolated from the wild relative of chickpea at low temperatures (9–15°C), successfully nodulated chickpea, indicating that it could serve as a potential microbial inoculant under low temperature conditions to maintain the normal functioning of plants. Symbiotic association of rhizobium with alfalfa enhances its tolerance to low temperature by regulating important physiological and metabolic processes. The oxidative enzymes were more active in AN (active nodules) and IN (inactive nodules) groups, providing higher cold tolerance to these plants [144].

4.2.3 Oxidative stress

Plants, in response to various kinds of environmental stresses such as biotic and abiotic stress produce reactive oxygen species (ROS). Examples of ROS are singlet oxygen ($^1O^2$), superoxide anion (O^{2-}), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH-). Accumulation of reactive oxygen species (ROS) as a result environmental stress is detrimental for plant growth as they modify the primary cell constituents like DNA, lipids, proteins etc. [145]. PGPR reduce the deleterious effects of ROS by producing antioxidant enzymes [146, 147] which include peroxidase (POD), superoxide dismutase (SOD), catalase (CAT), nitrate reductase (NR) and glutathione reductase (GR) and thus help in maintaining plant growth and crop productivity [148]. Based on the results of Shen et al. [149] it could be concluded that due to the activation of antioxidant machinery by the rhizobium inoculants, their use is the most effective way for enhancing plant growth and mitigating stress induced by ROS.

4.2.4 Metal stress

Heavy metals occur naturally in soils; however, their increased quantity is undesirable and has become a global concern over the time [150]. Anthropogenic activities like atmospheric pollution, industrial waste disposal, mining, and other practices predominantly contribute to heavy metal toxicity [151]. Heavy metal toxicity leads to inhibition of chlorophyll biosynthesis and proteins required for proper growth of plants and their normal functioning. Plant growth promoting rhizobacteria have the ability to control heavy metal pollution of soils as well as enhancing plant growth in these soils [152]. Bacteria's producing siderophores promote plant growth besides enhancing their nutrient uptake potential under heavy metal stress conditions. Rhizobacteria have been found to release metal-chelating substances (siderophores) in rhizosphere by means of which they affect the bioavailability of toxic heavy metals and their uptake by plants significantly. They transform these compounds into a less toxic form and promote their precipitation, absorption or adsorption. Plant associated rhizobia can be used for bioremediation, as they enhance the phytoextraction and phytostablization potential of plants [153]. By phytoextraction, plants carry the contaminants from the soil with the help of their roots and eventually collect these contaminants in the aboveground parts of the plant [154]. Phyto-stablization on the other hand, immobilizes the soil contaminants. The contaminants either get adsorbed on the root surface or absorbed by the roots or they are transformed into less soluble compounds. Phytoremediation has been accelerated by the application of rhizobacterial species such as *Bacillus*, *Pseudomonas, Azotobacter* [155]. Thus, efficient bioremediation is possible by using rhizobacterial inoculants, still distribution and functioning of microbes in rhizosphere needs to be fully explored.

5. Conclusion and future prospective

Rhizobia have enormous potential in terms of innovative and more sustainable crop management approaches; yet, we only comprehend a small portion of this potential. The effectiveness of strains of rhizobia documented in this chapter emphasizes the unique qualities of plant growth induction, defense pathways, and the resilience spectrum available against different environmental stresses on a wide range of agricultural crops. Although it is the most investigated bacteria which finds its application in agriculture practices but only few strains are widely known for their efficiency and effective application in disease management, nutrient uptake and signaling compounds they produce. These are often used for promoting plant development, particularly in challenging situations like heat and drought, which are becoming more common as climate change proceeds. The discovery of such possible rhizobia strains, as well as the development of a viable technology for use by agricultural producers, are still in their early stages. Thus, we conclude that a definite and real improvement in the long term lies with the use of advanced analytical tools and their unification with classical experimental techniques to comprehend and then further exploit soil–plant-microbe associations for ecofriendly and enhanced crop production. The identification of such promising rhizobia strains would allow for the extension of this study area, as well as improved agricultural sustainability.

Conflict of interest

The authors declare no conflict of interest.

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