



Bacterial associations with rice plants: Their diversity, abundance and importance in rice life cycle

Protup Kumer Sarker^{1*}, Dola Karmoker² and Anik Kumar Saha³

¹Infectious Diseases Division, International Centre for Diarrhoeal Disease Research, Bangladesh (icddr,b), Dhaka 1212, Bangladesh. E-mail: protup_du_bmb@yahoo.com

²Department of Biochemistry and Molecular Biology, University of Dhaka, Dhaka-1000, Bangladesh. E-mail: dola_karmoker@yahoo.com

³Department of Biochemistry and Molecular Biology, University of Dhaka, Dhaka-1000, Bangladesh. E-mail: anikshahamb@gmail.com

Article Info

Volume 4, Issue 2, April 2022

Received : 04 October 2021

Accepted : 17 March 2022

Published : 05 April 2022

doi: [10.33472/AFJBS.4.2.2022.1-18](https://doi.org/10.33472/AFJBS.4.2.2022.1-18)

Abstract

Global rice production is needed to be improved for ensuring food security in the coming decades. Prospective utilization of beneficial bacteria can be attributed as sustainable agricultural practices for the enhancement of the physiology of rice plants. This review focuses on and amalgamates the experimental findings where bacteria can assist the rice plant for better phenology. Bacteria in the rhizosphere are abundant and diverse compared to the bacteria in the endosphere and phyllosphere region of rice plants. Bacteria derived phytohormones can be utilized by rice plants to enhance phytohormone signaling for beneficiary purposes. Salicylic Acid (SA) may induce Systemic Acquired Resistance (SAR) to the rice plant to eradicate pathogen attack. Moreover, bacteria modulated Jasmonic Acid (JA)/Ethylene concentrations can assure Induced Systemic Resistance (ISR) for plant immunity. Some plant growth promotional activities of bacteria such as Biological Nitrogen Fixation (BNF), siderophore production, mineral solubilization are addressed in this worthwhile discussion. Abiotic stresses include drought, salinity, high and low temperatures, affects severe loss in rice production annually. The utilization of plant growth-promoting bacteria is the well-established solution for evading abiotic stresses by initiating or inhibiting various signaling processes as well as improvement of the yield of rice.

Keywords: Abiotic stress, Bacteria diversity, Biotic stress, ISR, SAR, Yield

© 2022 Protup Kumer Sarker et al. This is an open access article under the CC BY license (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

1. Introduction

In recent years, numerous studies target the response of biodiversity due to climate change, which has become one of the most concerning points of the current century. Experiments conducted at the beginning of the 21st century have a crucial role in alerting scientists and ecologists to figure out future risks and potential strategies to minimize the impacts of climate change on biodiversity (Bellard et al., 2012). Moreover, the population outburst has led to the disturbance of the homeostatic nature of the environment. Biodiversity reduction has

* Corresponding author: Protup Kumer Sarker, Infectious Diseases Division, International Centre for Diarrhoeal Disease Research, Bangladesh (icddr,b), Dhaka 1212, Bangladesh. E-mail: protup_du_bmb@yahoo.com

become a major issue for food scarcity, and the food production should be increased significantly to meet the demand of the mammoth population worldwide (Tkacz and Poole, 2015; Sarkar et al., 2018).

Rice (*Oryza Sativa*) is considered the most crucial cereal crop and staple food for more than half of the world's total population (Habibi et al., 2019). Global demand for rice is estimated to enhance from 439 million tons in 2010 to 555 million tons in 2035. If the world market is to be stabilized for the billions of consumers, global rice yield should rise faster. According to the Food and Agriculture Organization (FAO), currently 38.7% of the world's land area is utilized as agricultural land, among them 28.43% of the land is arable (Gouda et al., 2018). But environmental damage is heightening as a consequence of rapid urbanization and industrialization, resulting in the farmable land to rapidly decrease every year (Goswami and Deka, 2020; Gouda et al., 2018).

Since, the size of arable land can't be expanded, the pressure for the rice over-production is forwarded to wide-ranged utilization of chemical fertilizers as the plant nutrient which generally pose an environmental hazard for arable lands (de Souza et al., 2015). In the last few years, the stagnation and declining trends in yields in the rice cropping system have been reported to be mainly due to over-exploitation and mismanagement of soils threatening the sustainability issue of the rice cropping management system in the world (Bhatt et al., 2016). In other cases, deleterious abiotic stresses (like high salinity, drought, and high and low temperature, etc.) and biotic stresses (infections caused by virus, pathogenic bacteria, fungi, etc.) result in a considerable decrease in quality and quantity of rice production (Goswami and Deka, 2020; Chen et al., 2020).

Researchers have proposed various techniques till date for improving agriculture such as sustainable management practices, agricultural intensification, genetically engineered crops, and use of PGPM (Plant Growth-Promoting Microbe) as bio-fertilizers (Gouda et al., 2018). PGPM is consortium of microbial communities which includes bacteria, fungi, protozoa, archaea, etc. Plant microbiomes could play a lot of beneficial role to the host plants such as enhance the capacity of plants to acquire nutrients from the soil, reduce the excessive utilization of chemical fertilizers, modulates the level of hormone within the plant tissues, improve growth, health and production as well as adaptive advantage to the plants (Orozco-Mosqueda et al., 2018). Several previous studies have shown that microbiome diversity enhances biological control of host plants against diseases through Induced Systemic Resistance (ISR) and relieve abiotic stresses by modifying plant endogenous hormone and relative protein expression (Liu et al., 2018).

Among PGPM, this review focuses on the evaluation of Plant Growth Promoting Bacteria (PGPB) for the alleviation of abiotic and biotic stresses as well as the promotion of rice yield with a brief overview of how the bacterial diversity modulates the mechanism of survival capacity of rice under several changing climate conditions. As the diversity and composition of soil bacteria influence a wide range of ecosystem processes, many efforts have been directed toward understanding the microbial biogeography to the rice (Imchen et al., 2019). So, in this review, we are trying to amalgamate the comprehensive information on the utilization of beneficial PGPB for obtaining healthier and more productive rice plants even under different abiotic and biotic stresses.

2. What are PGPB? their classification

The bacteria populations colonize into or outside of the host plants and augment the growth of the plants through different direct and indirect mechanisms are termed as PGPB (Grover et al., 2011). The majority of the PGPB colonize into the root surface and move in space between root hairs, some are found in the root exudates, and some enter into the root tissues. Root exudates are an integral part of rhizosphere signaling events and regulate communication of beneficial plant-microbe interactions. Plant roots allow the entry and/or adherence of PGPB. Phenols, flavonoids, and organic acids secreted by roots have been known to act as chemical signals for bacterial colonization. PGPB can be classified into two main categories (i) Extracellular PGPB, which inhabit on the plant (Rhizoplane, the surface of the plant root and/or stem are generally termed as Associative/ Phyllospheric bacteria) or outside the plant (Rhizosphere, a narrow zone of soil where microbes are found in high concentrations, known as Rhizobacteria), (ii) Intracellular PGPB which inhabit inside the plant (Endosphere, the internal regions of plant tissues, known as Endophyte) (Gouda et al., 2018; Ilangumaran and Smith, 2017).

3. Regional diversity and abundance of PGPB throughout rice life cycle

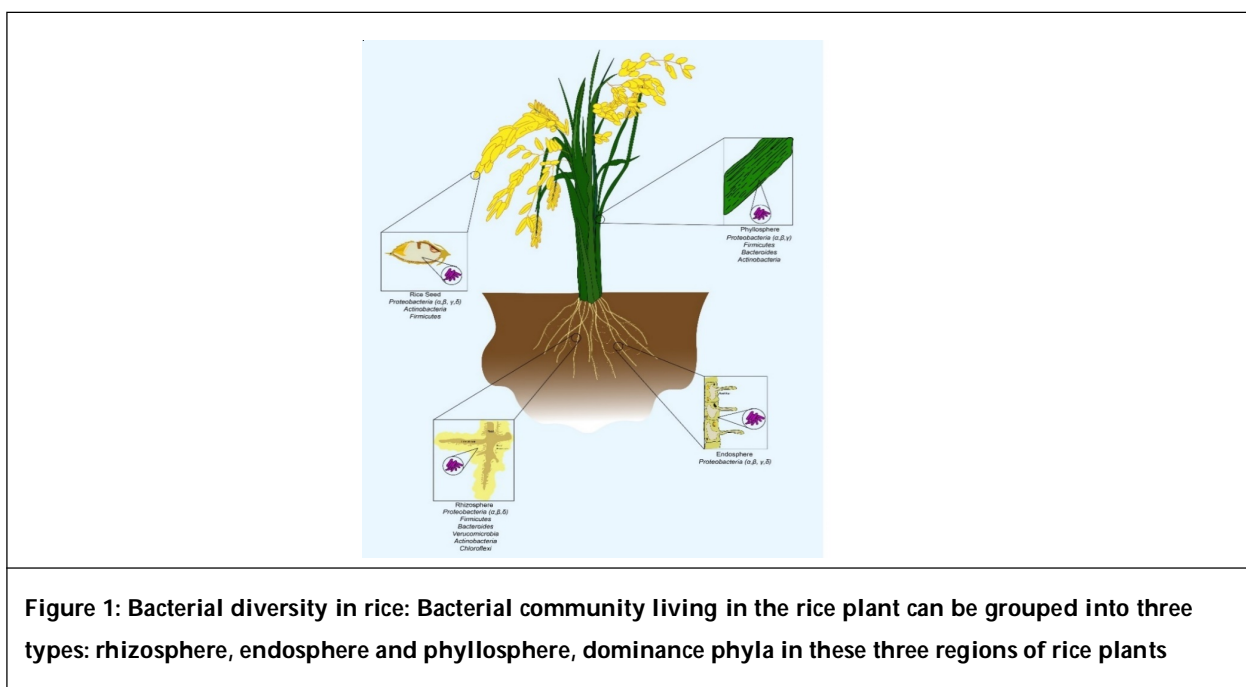
The patterns of bacterial communities in the rice rhizosphere regions are shaped by geographic location of host plant, physicochemical properties of soil, and rice genotype/phenotypic plasticity (Santos-Medellin et al., 2017). Modification of any described condition can alter soil environments for microbial growth, diversification and proliferation (Souza et al., 2013). It is essential to study microbial diversity and their dynamic relationship with rice plant for the demonstration of successful plant-microbe interaction to enhance crop performance (Figure 01) (Edwards et al., 2018).

3.1. Bacteria diversity at rhizosphere region

During the rice life cycle, root exudates pose dynamic changes of microbial flora (Edwards et al., 2015). To understand soil microbial ecosystems and complex microbial assemblages of a rice cropping system, bacterial 16S rRNA genes (hypervariable regions) were selected for analyzing bacterial Operational Taxonomic Units (OTUs) (Wang et al., 2019; Wang et al., 2016). A plethora of high-throughput sequencing-based studies were analyzed to understand the exact taxonomic information of bacterial communities in the rice rhizosphere. The presence of beneficial bacterial community is largely occupied by *Proteobacteria* (mainly *Alpha*-, *Beta*- and *Delta*-*proteobacteria* classes), *Firmicutes*, *Bacteroidetes*, *Verrucomicrobia*, *Actinobacteria*, *Chloroflexi*, and several other phyla (Jha et al., 2020). Undoubtedly, the bacterial community composition and diversity in the rice rhizosphere is distinct from that in the rhizosphere of other plants (i.e., maize, soybean, potato, populus and arabidopsis) which has been proved by some selected studies. Among them, the rice rhizosphere is found to be markedly enriched significantly with *Delta*-*proteobacteria* class while compared with rhizosphere region of other crop plants. Moreover, *Alpha*- and *Beta*-*proteobacteria* classes are also enriched in the rice rhizosphere (Raaijmakers and Mazzola, 2012).

3.2. Bacteria diversity at endosphere region

Rice root endosphere is enriched with *Beta*-*proteobacteria* and *Delta*-*proteobacteria* classes compared to the bulk soil and *Proteobacteria* dominated the rice endosphere microbiota which covered 71% and 87% of the total endosphere bacterial OTUs of the two rice cultivars (Edwards et al., 2018; Moronta-Barrrios et al., 2018). Walitang et al. (2017) coined a crucial study on 6 South Korean rice cultivars to assess bacterial endophytic community in the rice seeds. The 16S rRNA gene identification of these cultures revealed that major endophytes in the rice seeds belong to the classes *Alpha*-*proteobacteria*, *Beta*-*proteobacteria*, *Gamma*-*proteobacteria*, *Actinobacteria* and *Firmicutes*. However, rice seeds act as a vector for transmission of these rice associated endophytes colonizing different parts of the rice plants. Edwards et al. (2015) also reported that the endosphere microbiota reaches a steady state over a specific time period and their establishment in the endosphere region of rice plant is depended on the growth stage of rice plant during its' whole life cycle (Edwards et al., 2015).



3.3. Bacteria diversity at phyllosphere region

Analysis of bacterial community composition in the rice phyllosphere revealed the dominance of *Alpha-proteobacteria* (35%) and *Actinobacteria* (38%) in the phyllosphere of rice cultivar IR-72 (according to 16S rRNA gene-based community analyses) (Knief et al., 2012). Moreover, *Bacteroidetes*, *Firmicutes*, *Beta-* and *Gamma-proteobacteria* contributed mainly to the phyllosphere bacterial community (Bulgarelli et al., 2013).

Based on OTUs analyses and diversity indices, the robustness and species diversity remained significantly higher in the rhizospheres compared to the endosphere and phyllosphere region of rice cultivars (Moronta-Barrios et al., 2018). In the rhizosphere, more phyla were found increasing rather than decreasing over the life cycle. But the inverse situation was observed for bacteria present in the endosphere where a percentage of phyla in relative abundance were more prominent in the early stages of rice life and further decreased in abundance over the life cycle of the rice plants (Edwards et al., 2018). In rhizosphere, the microbes colonizing in later developmental stage are more conserved than early colonizing microbiome (Wu et al., 2018; Edwards et al., 2015). A more pronounced conservation and stabilization of the adult microbiome has been observed in the endosphere and phyllosphere compared to the rhizosphere (Edwards et al., 2018).

4. Plant growth promotion by phytohormone signaling

Beneficial microbiota can modulate plant hormone status by releasing exogenous hormones and increasing the physiological status of rice (Egamberdieva and Kucharova, 2009). Microbial derived phytohormones can mediate several processes such as plants cell division and enlargement, modulate physiological status during both normal and stressed condition (Glick, 2014).

Auxin: Auxin is a crucial phytohormone that plays a cardinal role in cell division, root growth and development, root initiation, root growth inhibition, phototropism, and apical dominance. Approximately, eighty percent of bacteria isolated in the rhizosphere region of some plants gained the capability to produce auxin as a secondary metabolite (Kumar et al., 2015). Auxin biosynthesis is occurred by multiple pathways and among them, one mechanism is the transformation of tryptophan to Indole Acetic Acid (IAA) which is easily absorbed by root exudates. In the plant tissues, due to abundant IAA molecules, the auxin signaling pathway is triggered to required production (Ilangumaran and Smith, 2017; Ambreetha et al., 2018; Kumar et al., 2015). Bacterial derived IAA can loosen the root cell wall and rhizosphere bacteria get nutrients and metabolite from root tissues (James et al., 2002). Bacterial IAA attract and allow more beneficial microbiota for entering into the plant tissues via root tips for the establishment of endophytic bacteria (Etesami et al., 2015). A significant study was designed to focus the role of bacteria derived IAA on the development of rice root biomass. The rice plants were inoculated with IAA-overproducing mutants of *Burkholderia cepacia* (RRE25), showed the development of proliferated root system than the plants inoculated with wild type strain or the un-inoculated plants. By synthesizing auxin, PGPB can directly modify rice root morphology, and the nutrient acquisition might be enhanced to a greater extent for the growth of rice (Singh et al., 2013).

Cytokinin: Cytokinin (CK) a group of adenine-derived phytohormones that regulate diverse mechanisms of plant physiological aspects such as proliferation of cell division, significant root phenotyping, accumulation of chlorophyll, leaf expansion, and shoot initiation etc (Li et al., 2019; Karnwal and Kaushik, 2011). Cytokinin production have been reported in PGPB, belonging to diverse genera such as *Pseudomonas*, *Azospirillum*, *Bacillus*, *Proteus*, *Klebsiella* and *Pseudomonas* isolated from a wide range of plant species (Persello-Cartieaux et al., 2001; Karnwal and Kaushik, 2011). Previously a significant study was designed to evaluate the role of *Methylobacterium* strains for rice. Results showed that the experimented bacteria were capable to increase germination rate and the amount of cytokinin and auxin in the bacteria treated rice plants (seedlings) than untreated control one. The experiment supported the idea (Holland, 1997) that cytokinin are produced by bacteria those rapidly colonize at the juvenile plant after germination and are barely produced into the plant cells (Lee et al., 2006). Raja et al. (2006) conducted a study to investigate the significant effect of individual and microbial consortium *Azospirillum lipoferum* Az-204, *Bacillus megaterium*, *Pseudomonas fluorescens* on rice exudates. They found that microbiome consortium enhances plant growth positively by synergistic mechanisms when compared to single inoculants application. Through the biochemical analysis of rice root exudates, IAA and Cytokinin amount was found to be significantly higher in the consortium treatments compared to the individual one.

Ethylene: Ethylene (ET), a gaseous plant hormone, is slowly diffusible in plant tissues while exerting its effects on plant developmental, defense and symbiotic processes. Ethylene biosynthesis into the plant is initiated by internal developmental signals and exogenous signals resulted from biotic and abiotic environmental factors

(Nascimento et al., 2018; Zhou et al., 2019). Ethylene concentrations are regulated by the precursor's 1-aminocyclopropane-1-carboxylate (ACC) (Nascimento et al., 2018). In rice, ethylene positively regulates grain size or weight, flowering, tillering and leaf angle but negatively affects rice grain filling and also causes early plant senescence (Zhou et al., 2019). Under extreme environment, occurrence of excessive ACC synthesis due to external stimuli is involved in initiating senescence, chlorosis and leaf abscission which ultimately leads plant to death (Glick, 2014). The presence of ACC deaminase in bacterial cells can cleave ACC to produce ammonia and α -ketobutyrate reducing the amount of excessive ethylene that the plant synthesizes during stress conditions (Yin et al., 2017; Steffens, 2014). One study was designed to evaluate the effectiveness of bacteria containing ACC deaminase for enhancing salt tolerance and improving the growth of rice plants under severe salt-stressed condition. Inoculation with the ACC deaminase containing strains *Alcaligenes* sp., *Bacillus* sp. and *Ochrobactrum* sp. reduced endogenous ethylene production by 90.2%, 81.6% and 81.5%, respectively compared to the negative control (Bal et al., 2013). Another crucial study conducted by Chinnadurai et al. (2009) revealed that phyllospheric bacteria *Methylobacteria* produced the enzyme ACC deaminase, reduce the stress ethylene level (60–80%) in rice plant, enhanced the root and shoot length of rice seedlings under gnotobiotic condition.

Abcisic acid: Abscisic acid (ABA) is a crucial phytohormone that is involved in synthesis of seed storage proteins and lipids, gene expression regulation, stress-related protein biosynthesis, stomatal closure, and promotion of seed desiccation tolerance (Ye et al., 2012). ABA mainly promote defense response by applying antagonistic interaction with Salicylic acid (SA) and Jasmonic acid (JA) /ethylene or additive interaction with JA, a very crucial aspects in plant immunity (Sahoo et al., 2014). ABA induces synthesis of compatible osmolytes, Late Embryogenesis Abundant (LEA) like proteins and help reduce stress damage in plants ultimately increasing plant stress tolerance. During stressed conditions, the bacterial ABA production might sustain the internal ABA pool in plants, alleviating the negative effects of the imposed stress (Cassán et al., 2014; Shahzad et al., 2017). By utilizing gas chromatography-mass spectrometry, ABA production was detected for *Bradyrhizobium japonicum* USDA110 (0.02 μ g/ml) and *Azospirillum. brasilense* Az39 (75.0 ng/ml) in two studies (Boiero et al., 2007; Cassán et al., 2009). A crucial study was coined using high-performance liquid chromatography (HPLC) technique to investigate phytohormone synthesis in several bacteria. Result showed the presence of ABA production in the culture medium of *Proteus mirabilis*, *P. vulgaris*, *Klebsiella pneumoniae*, *Bacillus megaterium*, *Bacillus cereus*, and *Escherichia coli* (Karadeniz et al., 2006). ABA producing isolates of *Azospirillum* spp. were obtained from the rhizospheric regions of rice fields near Khandagiri India which further were proved to elevate endogenous nutrient content, improve growth and yield physiology of rice plants compared to other treatments (Sahoo et al., 2014).

5. Phytohormonal role to strengthen rice immunity

The rice plant usually gets infected by a various number of pathogens which causes 10-15% global yield losses. For plant induced immune responses, the first step is the mechanism to recognize the pathogen (Malukani et al., 2019). Recognition is initiated by some signature molecules produced by bacterial and fungal pathogens which triggers immune responses upon perception are termed as Pathogen or Microbial Associated Molecular Patterns (PAMPs or MAMPs). Recognition of highly conserved MAMPs or PAMPs by plant tissues transmembrane pattern recognition receptors (PRRs) leads to MAMP-triggered immunity (MTI) or PAMPs-triggered immunity (PTI) that restricts pathogen attack to the host tissue (Gimenez-Ibanez et al., 2016). Moreover, another type of mechanism behind the innate immunity in plants, which becomes effective upon recognition of highly variable microbial molecules (also known as effectors), is known as effector-triggered immunity (ETI) (Spoel and Dong, 2012).

Downstream to ETI or PTI mechanisms, the activation of intra phytohormones signaling networks stimulates plant immune signaling network. JA and SA play a central role (Yang et al., 2015). SA and JA mediated defense pathways usually antagonize each other for developing resistance against biotic stress. The SA signaling positively enhance plant immunity against biotrophic pathogens that usually feed and reproduce on living host cells. On the other hand, the JA/ET pathways are necessary for plant immune resistance against necrotrophic pathogens and herbivorous insects which derive nutrients from living host cells (Figure 02) (Gimenez-Ibanez et al., 2016). It has been suggested that SA is a master regulator of pathogen-induced Systemic Acquired Resistance (SAR), whereas JA and ET are indispensable for PGPB mediated ISR. Usually, PGPB induce ISR in rice or every model plant and ISR is effective against different types of pathogens but differs from SAR. The differences occur due to the antagonistic role of SA and JA. It is manifested that beneficial microbe

inhabits in the root exudates induce ISR in model plants. But some studies also reported exogenous synthesis of SA by PGPB and this synthesis directly helps the model plant for defense response through inducing ISR and SAR in plants (Gupta et al., 2020).

There are few reports under pathogenic condition where root colonization by PGPB was shown to synthesize SA as for the secondary metabolites, which eventually induced plant systemic resistance and upregulated the plant's basal defense mechanisms (Kandaswamy et al., 2019; Rekha et al., 2020). The role of PGPB synthesized SA for augmenting plant immunity was reported for *Pseudomonas aeruginosa* 7NSK2 and its SA producing mutant (Patel et al., 2016). Systemic resistance induced by some *Bacillus* strains requires SA dependent pathways, despite different strains of *Bacillus* sp. operate through an ET/JA-dependent mechanism similarly to *Pseudomonas fluorescens* WCS417r (Patel et al., 2016). A study reported an increased concentration of SA in plants due to the treatment of *Bacillus pumilus* (Zhang et al., 2002). Some study also reported *Acinetobacter* sp, *Pseudomonas* sp, and *Serratia* sp, have higher potentiality for SA production (Gupta et al., 2020). Previous studies confirmed that, root inhabiting endogenous PGPBs like *Pseudomonas aeruginosa*, *Bacillus licheniformis*, *Bacillus cereus*, *Bacillus mycoides*, *Bacillus pumilus*, *Bacillusphaericus* and *Bacillus subtilis*, *Pseudomonas fluorescens*, *Serratia marcescens*, *Burkholderiacepacia* etc. have capacity for synthesizing SA *in vitro* and also provide role in plant growth and development as well as survival capacity under adverse condition (Gupta et al., 2020). Although PGPB normally induce ISR in the model plant, SAR was also reported to be induced by nonpathogenic beneficial bacteria by synthesizing endogenous SA upregulating transcript related SA biosynthesis in various plant species including rice plant (Kandaswamy et al., 2019; Rekha et al., 2020).

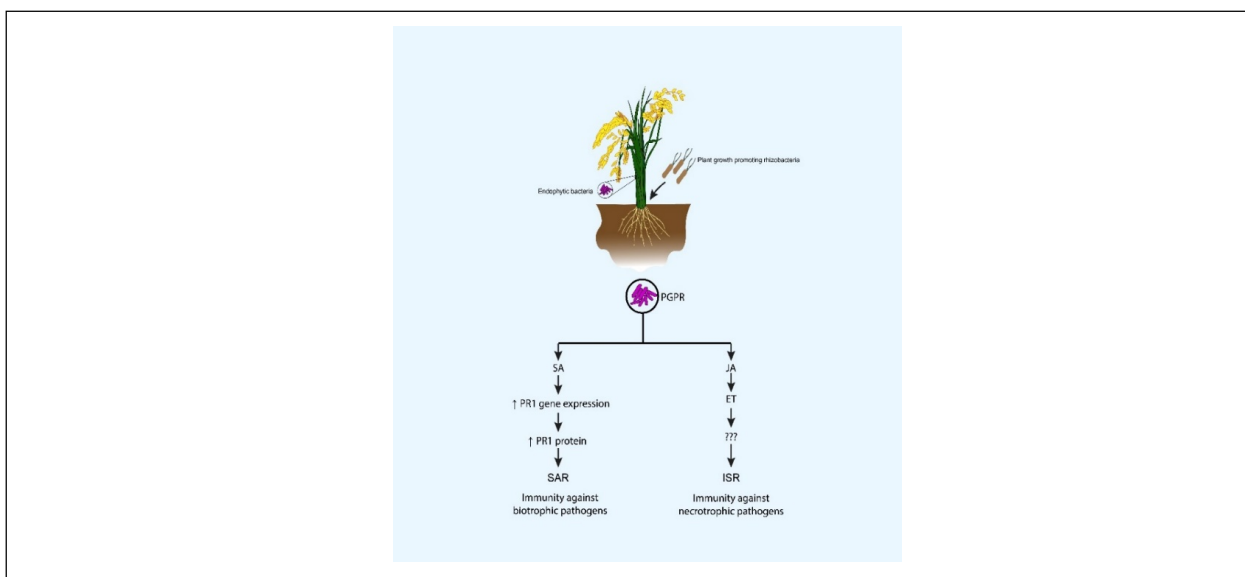


Figure 2: Phytohormonal regulation on immunity: Phytohormonal control on immunity against biotic stress achieved by Salicylic Acid and Jasmonic Acid mediated defense pathways. SA is the key player in SAR whereas ISR is mediated by JA. SAR involves PR-1 proteins which show antimicrobial action. On the other hand, JA and Ethylene become induced in induced systemic resistance. PGPB turn on SA and JA pathways and trigger rice plant to show immunity against attack by biotrophic and necrotrophic pathogens respectively. SA: Salicylic acid, JA: Jasmonic acid, ET: Ethylene. '?' indicates unidentified protein.

6. Beneficial characteristics possessed by PGPB

Biological Nitrogen Fixation (BNF): BNF is the process of reduction of dinitrogen from the air to ammonia carried out by a large number of species of free-living and symbiotic microbes in both leguminous and non-leguminous plant called Diazotrophs. Diazotrophic bacteria can also take up nitrogen from nitrate and nitrite constituents of soil and fertilizers through reduction by nitrate and nitrite reductase and also from biologically fixed and chemically converted nitrogen (Canfield et al., 2010). Several bacterial species including *Azotobacter*, *Clostridium*, *Azospirillum*, *Herbaspirillum*, *Burkholderia* and *Rhizobium* can supply nitrogen to rice plants by BNF and increase rice grain yield (Biswas et al., 2000; Rima et al., 2018). *Azotobacter* sp. comprises of the principal group of heterotrophic free-living nitrogen-fixing bacteria and plays crucial role for improving productivity of the non-leguminous crops. Rice plants treated with *Azotobacter vinelandii* SRIAz3 are found to

be contained higher level of compatible solute, plant hormones and macronutrients, resulting in better growth of root and shoots and thereby improved tolerance to salinity compared to other treatments (Sahoo et al., 2014). *Azotobacter chroococcum* inoculation into rice results in positive response in several growth parameters in terms of shoot length, root length, shoot dry and fresh weight, root fresh weight and panicle number both at vegetative and reproductive stages. *Azospirillum lipoferum* shows maximum nitrogen fixation for super basmati variety measured by N^{15} isotropic dilution method in greenhouse condition (Sahoo et al., 2014).

Phosphate and zinc solubilization: P-Solubilizing Bacteria (PSB) comprise 1-50% of the total representative population of the soil (Gyaneshwar et al., 2002). Bacteria from the genus *Bacillus*, *Rhodococcus*, *Arthrobacter*, *Serratia*, *Chryseobacterium*, *Delftia*, *Gordonia* and *Phyllobacterium*, generally show phosphate solubilization activity (Chen et al., 2006). *Bacillus* spp PSB16 strain inoculation in aerobic rice plant results in P solubilization (24.08 mg kg⁻¹) and increased plant P uptake (5.31 mg plant⁻¹) at the highest P level of 60 kg ha⁻¹ (Panhwar et al., 2011). Following treatment with two *Bacillus* spp., soluble P, plant P uptake and organic acid concentration in roots were significantly increased in aerobic rice variety after 60 days (Panhwar et al., 2011). Rice plants inoculated with PSB *Burkholderia seminalis* were observed with greater plant height (18 cm) and dry biomass (0.76 g) and also there was an increase in a bunch of parameters such as root length, surface area and volume in inoculated plants compared to un-inoculated rice plants (Panhwar et al., 2014).

Rice is delicate to Zn deficiency and consequently causes malnutrition to most of the rice-eating Asian populations (Krithika and Balachandar, 2016). PGPB inoculation abated Zn deficiency syndrome as indicated by the increase in total biomass (23%), grain yield (65%), harvest index and Zn concentration in the soil (Tariq et al., 2007). Zn solubilizing *Bacillus* spp. and *Bacillus cereus* strains significantly improved the translocation of Zn to grains and improved yields of rice variety Basmati-385 and Super Basmati by 22-49% and 18-47% respectively (Shakeel et al., 2015). Multiple *Pseudomonas* strains were reported to account for almost 1.5- to 2-fold increase in Zn content in roots, shoots as well as grains of rice plant (*Oryza sativa* L.) in comparison to the control and showed improvement in rice growth and yield (Sharma et al., 2015). *Burkholderia* and *Acinetobacter* strains significantly increased the total Zn uptake/pot (52.5%) along with grain methionine concentration (38.8%) in rice (Vaid et al., 2014).

Siderophore production: Iron (Fe) is an essential micronutrient for all living organisms in the soil, but its availability is often limited (Tariq et al., 2017). Siderophores can bind to Fe³⁺, transport it back to microbial cells and make it available for microbial growth (Meyer, 2000). Siderophores are sometimes secreted by PGPB, ultimately taken up by plants, therefore, transporting a molecule of iron to the plant's cells. Plant roots can take up siderophore and utilize them as the iron sources (Sharma and Johri, 2003).

Many researchers have reported the siderophore production in a wide range of bacterial species like *Bacillus*, *Pseudomonas*, *Azotobacter*, *Arthrobacter*, *Burkholderia*, *Enterobacter*, *Rhodospirillum*, *Serratia*, *Azospirillum* and *Rhizobium*. In the rhizosphere region, PGPB derived siderophore have dual functionality: (a) Siderophores can improve plant growth by increasing plant nutrient availability through iron uptake. (b) Beneficial bacteria-derived siderophore prevents the growth of soil-borne pathogens causing iron limitation in the rhizosphere (Saha et al., 2016; Tariq et al., 2017; Delaporte-Quintana et al., 2020). A study was performed to observe the association of Siderophore Producing Bacteria (SPB) in *Oryza sativa* cultivated in Uruguayan soils. The author reported that rice roots were enriched in SPB than the surrounding soil (Loaces et al., 2011). For better understanding the beneficial effect of microbe derived siderophore for rice, a pot culture experiment was carried out where the siderophore-producing *Streptomyces* sp. GMKU 3100 which was isolated from the roots of Thai Jasmine rice plant, was utilized. The group developed a mutant of *Streptomyces* sp. GMKU 3100 deficient in siderophore production. In the pot culture experiment, the rice plants were treated with *Streptomyces* sp. GMKU 3100 wild type and mutant keeping bacteria untreated plant as base control and the Results revealed that rice plants inoculated with the wild type had the best enhancement of plant growth, root and shoot biomass compared to untreated controls and mutant treatments (Rungin et al., 2012).

7. PGPB on biotic stress tolerance of rice

To alleviate the negative effect of biotic stresses on the rice plant, PGPB offers potentially new biological control agents with a novel mechanism of disease suppression in the range of environment. The beneficial microbes either alone or in combinations can lower the doses of usage of harmful chemicals and environmental hazards needed to obtain a profitable crop yield (Lucas et al., 2014; Van Loon et al., 1998). The induction of ISR by beneficial microbiome mainly involves Jasmonate (JA) or/and Ethylene dependent signals, ISR is closely

related with the enhancement in sensitivity to these hormones may lead to the activation of the different set of defense genes (Figure 3) (Pieterse et al., 2001). According to the Lucas et al (2014) *Chryseobacterium* sp. and *Pseudomonas* sp. can augment ISR against *Xanthomonas campestris* by different mechanisms. *Chryseobacterium* sp. can significantly enhance Ascorbate Peroxidase (APX), Glutathione Reductase (GR) and Acyl-Homoserine Lactone (AHL) enzymes related to the detoxification of reactive oxygen species (ROS). While *Pseudomonas* sp. administration enhance pathogenesis-related proteins (PRs) such as β -1,3-Glucanase and chitinase are involved in defensive mechanism of rice plants against pathogen attack (*Xanthomonas campestris*). The siderophore produced by *Pseudomonas fluorescens* WCS374r to trigger ISR in rice against the leaf blast pathogen *Magnaporthe oryzae* was found to be an important determinant of ISR (De Vleeschauwer et al., 2008). *Bacillus amyloliquefaciens* (SN13) mediated biotic stress tolerance by enhancing the immune response against *Rhizoctonia solani* in rice through production of proline, mannitol, and arabinol, quinazoline and hormonal cross talk (Srivastava et al., 2016).

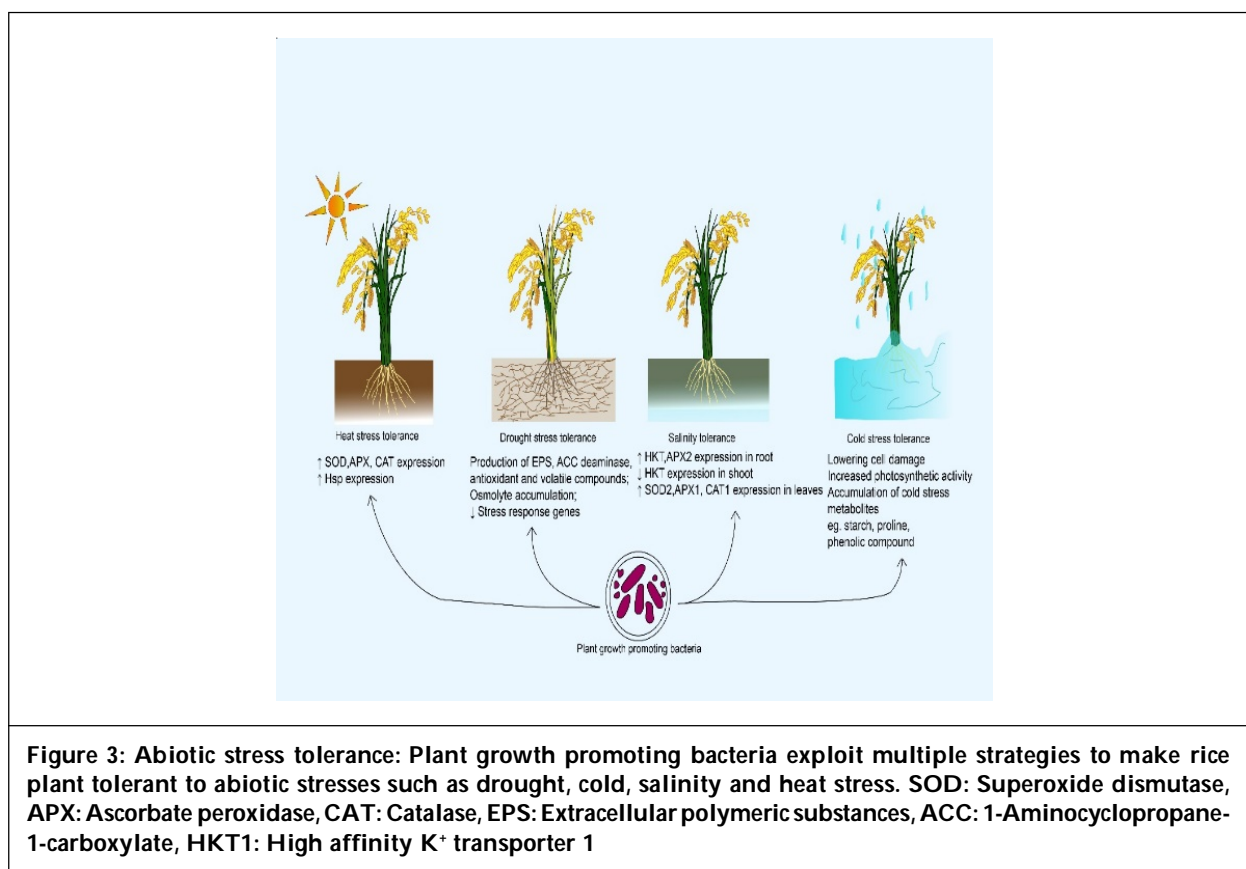
8. Effect of abiotic stress on rice growth and PGPB as an option for alleviation

Changing climate is a concerning issue in today's world and agriculture is considered to be the most vulnerable sector to it. Increased incidences of abiotic and biotic stresses are being witnessed all over the world and has become the major cause for the stagnation of productivity in principal crops. Extreme events like increased salinity, droughts, prolonged rains with flooding, heat waves, frost damages, elevated CO₂ and cyclones which are responsible for serious economic losses are likely to further increase as a result of climate change (Grover et al., 2011). Evolving such methods is a major challenge for stress management. Induced Systemic Tolerance (IST) is a term used for indicating PGPB-induced physical and chemical changes that makes the host plants tolerant to abiotic stresses. Researches claim that symbiotically conferred abiotic stress tolerance involves at least two mechanisms: (1) Activation of host's stress response after exposure to stress which allow plant to mitigate the negative impacts of the stress (Redman et al., 1999) and (2) Biosynthesis of some anti-stress biochemical by PGPBs for alleviating stress on host plant (Schulz et al., 2002). PGPB act as stress controller for associated plants (Lata et al., 2018). Beneficial bacteria can play significant roles in specific stressed environment by various stress-specific mechanisms.

Role on drought tolerance: Among all the abiotic stresses, drought stress is the most destructive one affecting the world's food security. The increased intensity of drought stress over the past decades has caused havoc plant growth problems and it is suspected that the problem will take over more than 50% of the arable lands by 2050 (Kasim et al., 2013). Drought is a multidimensional stress that affects different physiological, morphological, biochemical and molecular traits in plants ultimately leading to yield loss and plant death. Drought also increases the production of free radicals and ROS affecting antioxidant defenses resulting in oxidative stress (Vurukonda et al., 2016). To alleviate the negative impacts of drought stress, PGPB impose different mechanisms, production of different Extracellular Polymeric Substances (EPS), ACC deaminase, phytohormones, accumulation of osmolytes, antioxidants and volatile compounds, upregulation or downregulation of some stress-responsive genes, and modification in morphology of the root architecture, etc. (Figure 3) (Mohammadipanah and Zamanzadeh, 2019). To evaluate the beneficiary effect of bacteria for mitigating drought, *Gluconacetobacter diazotrophicus* Pal5 was inoculated on the red rice and the results showed that bacteria treated rice plants have increase in plant biomass, higher levels of gas exchange, synthesis of osmo-protective solutes, and defense genes (catalase (CAT), superoxide dismutase (SOD) and betaine aldehyde-dehydrogenase (BADH)). So *Gluconacetobacter diazotrophicus* Pal5 inoculation was beneficial for rice, minimizing the various deleterious effects of drought stress and increasing biomass and yield potential (Filgueiras et al., 2020). Narayanasamy et al. (2020) found that *Bacillus altitudinis* FD48 and *Bacillus methylotrophicus* RABA6 co-inoculated two rice cultivars have enhanced photosynthetic pigment, proline content and increased activity of ROS- quenching enzymes, thereby increasing drought resilience and growth augmentation in rice plant. Moreover, Increased relative water content, chlorophyll and membrane stability index, increased proline and phenolics content, catalase activity, reduced malondialdehyde (MDA) content, ethylene emission are observed in *Bacillus altitudinis* FD48 treated rice plants to evade drought stress (Aswathy et al., 2017). ACC deaminase producing bacterial consortium has been found to alleviate drought stress on model crops by down regulating ACC-oxidase gene expression (Saikia et al., 2018).

Salinity and alkalinity tolerance: Salinity is the second most disastrous stress that negatively impacts plant growth, development and yield. According to an estimate of the United Nations environment program, approximately 20% of agricultural and 50% of cropland around the world is affected by salinity stress (Flowers,

2004). It is suspected that 50% of the total agricultural area may be affected with salinity by 2050 (Yoo et al., 2019). Osmotic and ionic stress are the two major stresses that plants have to face as an effect of salinity. Osmotic stress causes dehydration and accumulation of salt in the soil surrounding plant root. Ionic stress causes an excessive influx of sodium ion and efflux of potassium ion leading to Na^+ toxicity inside plant cell (Orozco-Mosqueda et al., 2018). The salinity stress overall causes stomatal closure, decreased plant photosynthesis rate, constant production of ROS imposes oxidative stress on plants (Figure 3) (Ilangumaran and Smith, 2017). PGPB is known for their excellent stress mitigating properties, *Bacillus subtilis* GB03 has been reported to confer salt tolerance by tissue-specific regulation of *HKT1* (High affinity K^+ transporter 1) gene under salt stress resulted in lower Na^+ accumulation throughout the plant (Zhang et al., 2008). *Bacillus amyloliquefaciens* RWL-1 modifies the physiology of rice plants by upregulating of essential amino acids in plant as a response to stress, reduced endogenous ABA and increased SA in rice plant during saline condition (Shahzad et al., 2017). Sun et al. (2020) explored that rice seedling had been inoculated with *Pantoea alhagi* NX-11 exhibited higher amount of fresh weight, increasing root and shoot length, increasing chlorophyll contents and proline level, decreasing MDA level and produced large amounts of EPSs. So, it has been speculated that the ability of *Pantoea alhagi* NX-11 to enhance the salt tolerance of rice seedlings is related to the above explanations that PGPB evade the saline stress of rice plants by several mechanisms.



Heat tolerance: Increased heat stress as a result of global warming causes crop loss frequently. Plant photosynthesis is highly sensitive to heat stress and fluctuations in temperature severely reduce the rate of carbon assimilation (Kumar et al., 2019). Researchers are concerned with this issue and the researchers at the last two decades has revealed that plant thermos tolerance is regulated and governed by the casein lytic proteinase/heat shock protein 100 (ClpB/Hsp100). As evidence, arabidopsis mutants becomes extremely sensitive to heat when there is defect in ClpB/Hsp100 protein expression. Similar incidence has been observed in rice and maize mutant plants defective in ClpB/Hsp100 synthesis (Mishra and Grover, 2016). Beneficial bacteria respond with changing temperature and may impact on plant physiological status under heat stress. Wheat seed treatment with bacterial strains *Bacillus amyloliquefaciens* UCMB5113 or *Azospirillum brasilense* NO40 caused decreased expression of several stress related genes and lower response of ascorbate-glutathione redox cycle. Reduced generation of ROS, changes in metabolome profile and pre-activation of some heat shock transcription factors are some important mechanisms through which the bacterial strains helped the plant

(El-daim et al., 2014). So, searching for heat-tolerant bacteria which are capable of regulating and inducing the level of osmolytes in plants may take the study a step ahead to unrevealed how PGPB mitigate heat stress in rice plants (Figure 3).

Cold stress tolerance: Bacteria-mediated cold stress tolerance of rice cultivars is also not a well-studied area and need to be explored more. Cold stress imposes destructive impacts on plants life causing disruption of micro-organelle, dehydration of cells and tissues and production of ROS of concomitant oxidizing potential (Kazemi-Shahandashti and Maali-Amiri, 2018). Cold stress exerts different physiological, biochemical and molecular changes in plants (Figure 03) (Li et al., 2018). According to an experiment, the presence of consortium of two rhizobacteria *Bacillus amyloliquefaciens* Bk7 and *Brevibacillus laterosporus* B4 decreased leaf MDA content and electrolyte leakage, and increased leaf proline, SOD, CAT, and chlorophyll content. Moreover, up-regulated expression of *OsMYB3R-2*, *OsDIL*, *OsDREB1A* and *OsCDPK13* genes can play important roles to confer induced systematic tolerance, augment the physiology of rice plants subject to chilling and drought stress (Kakar et al., 2016).

9. Role of PGPB to enhance yield

Rice yield is determined by management practices, which must denote the productive capacity of a crop ecosystem. Rice is phonologically divided into vegetative stage (from emergence to panicle primordia initiation), reproductive stage (from panicle primordia initiation to flowering), and spikelet filling stage (from flowering to physiological maturity). Yield potential of rice is formed or defined during these growth stages. The reproductive growth stage is the most sensitive to biotic and abiotic stresses, followed by spikelet filling stage and vegetative growth stage (Fageria, 2007). Rice root-associated bacteria assembly is important for yield enhancement under both normal and drastic climate condition (Table 1). Bacterial community is a crucial descriptor of different stages of rice plant growth and survival capacity. According to Edwards et al. (2018), plant age and developmental stage are very crucial drivers of the root-associated bacteria (Edwards et al., 2018). The combination of physical (root structure morphology) and chemical (root exudation) modification contributes to the succession of the bacterial diversity. The differences between the bacterial community and functional gene expressions at different time period were found to be important regulators in enhancing rice yield (Wang et al., 2019).

Plant growth promoting bacteria	Yield enhancement	References
<i>Herbaspirillum</i> sp., <i>Burkholderia</i> sp.,	Enhancement of plant height, NPK uptake, dry shoot and grain production, though chemical fertilizer was diminished in half.	(Souza et al., 2013)
<i>Pseudacidovorax</i> sp., <i>Rhizobium</i> sp., <i>Azospirillum</i> sp., <i>Pseudomonas</i> sp., <i>Candida</i> sp., <i>Bacillus amyloliquefaciens</i> , <i>Bacillus subtilis</i>	Increasing grain and straw yields, total N uptake and grain quality in terms of percentage N. Nitrogen fertilization increased grain and straw yields as well as total N and P uptakes significantly in studied cropping seasons.	(Cong et al., 2009)
Seven rice endophyte strains of <i>R. leguminosarum</i> bv. <i>trifolii</i>	Inoculation with single strains or multi-strain consortia significantly promoted grain yield. Grain yield was increased up to 47% in field experiment.	(Yanni and Dazzo, 2010)
<i>Pseudomonas fluorescens</i>	Inoculation with mixture of PGPR (plant growth promoting rhizobacteria) strains to the rice plant significantly promoted grain yield. The average yield enhancement was 17.7%, for single strains and 25.9% in case of mixture.	(Nandakumar et al., 2001)

Table 1 (cont.)		
Plant growth promoting bacteria	Yield enhancement	References
<i>Bacillus</i> sp.	The bacteria reduced disease severity and increased yield as well as yield related parameters such as plant height, tillering, panicle length and yield.	(Rais et al., 2016)
<i>Lysinibacillus xylantilyticus</i> , <i>Alcaligenes faecalis</i> , <i>Bradyrhizobium japonicum</i> , <i>Rhizobium etli</i> , <i>Bacillus subtilis</i> ,	The significant effects of beneficial bacterial inoculations are appeared due to plant growth promotion activities. Isolated indigenous PGPR and rhizobial strains have the potentiality to increase growth and yield of rice by minimizing Nitrogen fertilizer use.	(Ali-Tan et al., 2017)
<i>Burkholderia</i> sp. <i>Pseudomonas aeruginosa</i>	Application of two most efficient phosphate solubilizing bacteria by root dipping (colonization) during seedling stage and administrating at the flowering stage significantly increased the growth and grain yield of rice variety BRRI dhan-29 with reduction of major fertilizers utilization.	(Khan et al., 2017)
<i>Pseudomonas</i> species, <i>Azotobacter chroococcum</i> and <i>Azospirillum brasilense</i> .	Combined application of RHB (Rice Husk Biochar) and PGPB, higher rice yield and uptake of nutrients in rice were significantly obtained.	(Singh et al., 2017)

Among the production practices, Water and Nitrogen (N) have especial importance in increasing rice yield. The significant effect of Nitrogen, Phosphorus, Potassium (NPK) and bacterial bio-fertilizer was evaluated in aerobic rice to find the beneficiary role bacterial bio-fertilizer. The treatments of bacterial bio-fertilizer along with NPK directly affect the rice morphological growth and yield as the combination was able to fix atmospheric nitrogen in the rice plants (Nasarudin et al., 2018).

To evaluate the performance of PGPBs as bio-fertilizers for increasing rice grain yield, rice plants were treated with bacteria non inoculants, single bacteria inoculant, bio-fertilizer inoculants (prepared with four diazotrophs) keeping uninoculated plants as controls. In both controlled pot experiment and different fields conditions, bio-fertilizers inoculants treated plants increased yield between 9.5 to 23.6%, while single inoculants alone increased yield by 5.6 to 12.16% over the un-inoculated control treatment (Govindarajan et al., 2008).

10. Conclusion

Changing climate is a threat to rice production and PGPBs could be an excellent alternative to the other harmful methods used to increase rice productivity. Exploring the properties of PGPBs will help in finding the best possible formulations for enhancing rice yield under adverse conditions. PGPBs are gaining popularity as biofertilizers nowadays and information of researches till done on PGPBs could help this process to be progressed faster. A lot have been explored and more to know yet. This review is aimed to highlight some such necessary information which would help the researchers in their scientific field of establishing sustainable agriculture. But the limitation of the review is that it only deals with exploring the beneficial effect of PGPBs to the rice plant. The question of how the PGPB augment and modify physiological status of rice plant remain unsolved. In the recent years, researchers are keen to utilize omics-based studies (Genomics, Transcriptomics, Proteomics) to identify the molecular mechanisms behind the beneficial interactions among rice and PGPB. Although this review can't provide the crucial information in view of molecular aspects, it will depict the positive interrelation among rice-PGPB interaction.

Acknowledgment

We are grateful to Professor Zeba Islam Seraj (PhD) [University of Dhaka] and Professor Md. Rakibul Islam (PhD) [University of Dhaka] for their continuous support towards us.

References

- Ali-Tan, K.Z., Radziah, O., Halimi, M.S., Rahim, K.B.A., Abdullah, M.Z. and Shamsuddin, Z.H. (2017). Growth and yield responses of rice cv . MR219 to rhizobial and plant growth-promoting rhizobacterial inoculations under different fertilizer-N rates. *Bangladesh Journal of Botany*, 46(1), 481-488.
- Ambreetha, S. et al. (2018). Plant-associated *Bacillus* modulates the expression of auxin responsive genes of rice and modifies the root architecture. *Rhizosphere*, 5, 57–66. doi: 10.1016/j.rhisph.2017.12.001.
- Aswathy, S.K., Sridar, R. and Sivakumar, U. (2017). Mitigation of drought in rice by a phyllosphere bacterium *Bacillus altitudinis* FD48. *African Journal of Microbiology Research*, 11(45), 1614–1625. doi: 10.5897/ajmr2017.8610.
- Bal, H.B. et al. (2013). ACC deaminase and IAA producing growth promoting bacteria from the rhizosphere soil of tropical rice plants. *Journal of Basic Microbiology*, 53(12), 972–984. doi: 10.1002/jobm.201200445.
- Bellard, C. et al. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15(4), 365–377. doi: 10.1111/j.1461-0248.2011.01736.x.
- Bhatt, B. et al. (2016). Long-term effects of fertilization and manuring on productivity and soil biological properties under rice (*Oryza sativa*)–wheat (*Triticum aestivum*) sequence in Mollisols. *Archives of Agronomy and Soil Science*, 62(8), 1109–1122. doi: 10.1080/03650340.2015.1125471.
- Biswas, J.C. et al. (2000). Rhizobial inoculation influences seedling vigor and yield of rice. *Agronomy Journal*, 92(5), 880–886. doi: 10.2134/agronj2000.925880x.
- Boiero, L. et al. (2007). Phytohormone production by three strains of *Bradyrhizobium japonicum* and possible physiological and technological implications. *Applied Microbiology and Biotechnology*, 74(4), 874–880. doi: 10.1007/s00253-006-0731-9.
- Bulgarelli, D. et al. (2013). Structure and functions of the bacterial microbiota of plants. *Annual Review of Plant Biology*, 64, 807–838. doi: 10.1146/annurev-arplant-050312-120106.
- Canfield, D.E., Glazer, A.N. and Falkowski, P.G. (2010). The evolution and future of earth's nitrogen cycle. *Science*, 330(6001), 192–196. doi: 10.1126/science.1186120.
- Cassán, F. et al. (2009). *Azospirillum brasilense* Az39 and *Bradyrhizobium japonicum* E109, inoculated singly or in combination, promote seed germination and early seedling growth in corn (*Zea mays* L.) and soybean (*Glycine max* L.). *European Journal of Soil Biology*, 45(1), 28–35. doi: 10.1016/j.ejsobi.2008.08.005.
- Cassán, F., Vanderleyden, J. and Spaepen, S. (2014). Physiological and agronomical aspects of phytohormone production by model Plant-Growth-Promoting Rhizobacteria (PGPR) belonging to the genus *azospirillum*. *Journal of Plant Growth Regulation*, 33(2), 440–459. doi: 10.1007/s00344-013-9362-4.
- Chen, C. et al. (2020). Global warming and shifts in cropping systems together reduce China's rice production. *Global Food Security*, 24, 100359. doi: 10.1016/j.gfs.2020.100359.
- Chen, Y.P. et al. (2006). Phosphate solubilizing bacteria from subtropical soil and their tricalcium phosphate solubilizing abilities. *Applied Soil Ecology*, 34(1), 33–41. doi: 10.1016/j.apsoil.2005.12.002.
- Chinnadurai, C., Balachandar, D. and Sundaram, S.P. (2009). Characterization of 1-aminocyclopropane-1-carboxylate deaminase producing methylbacteria from phyllosphere of rice and their role in ethylene regulation. *World Journal of Microbiology and Biotechnology*, 25(8), 1403–1411. doi: 10.1007/s11274-009-0027-1.
- Cong, P.T. et al. (2009). Inoculant plant growth-promoting microorganisms enhance utilisation of urea-N and grain yield of paddy rice in southern Vietnam. *European Journal of Soil Biology*, 45(1), 52–61. doi: 10.1016/j.ejsobi.2008.06.006.
- de Souza, R., Ambrosini, A. and Passaglia, L.M.P. (2015). Plant growth-promoting bacteria as inoculants in agricultural soils. *Genetics and Molecular Biology*, 38(4), 401–419. doi: 10.1590/S1415-475738420150053.

- Delaporte-Quintana, P. et al. (2020). The plant growth promoting bacteria *Gluconacetobacter diazotrophicus* and *Azospirillum brasilense* contribute to the iron nutrition of strawberry plants through siderophores production. *Plant Growth Regulation*, 91(2), 185–199. doi: 10.1007/s10725-020-00598-0.
- De Vleeschauwer, D. et al. (2008). *Pseudomonas fluorescens* WCS374r-induced systemic resistance in rice against *Magnaporthe oryzae* is based on pseudobactin-mediated priming for a salicylic acid-repressible multifaceted defense response. *Plant Physiology*, 148(4), 1996–2012. doi: 10.1104/pp.108.127878.
- Edwards, J. et al. (2015). Structure, variation, and assembly of the root-associated microbiomes of rice. *Proceedings of the National Academy of Sciences of the United States of America*, 112(8), E911–E920. doi: 10.1073/pnas.1414592112.
- Edwards, J.A. et al. (2018). Compositional shifts in root-associated bacterial and archaeal microbiota track the plant life cycle in field-grown rice. *PLoS Biology*, 16(2), 1–28. doi: 10.1371/journal.pbio.2003862.
- Egamberdieva, D. and Kucharova, Z. (2009). Selection for root colonising bacteria stimulating wheat growth in saline soils. *Biology and Fertility of Soils*, 45(6), 563–571. doi: 10.1007/s00374-009-0366-y.
- El-daim, I.A.A., Bejai, S. and Meijer, J. (2014). Improved heat stress tolerance of wheat seedlings by bacterial seed treatment. 337–350. doi: 10.1007/s11104-014-2063-3.
- Etesami, H., Alikhani, H.A. and Hosseini, H.M. (2015). Indole-3-acetic acid (IAA) production trait, a useful screening to select endophytic and rhizosphere competent bacteria for rice growth promoting agents. *MethodsX*, 2, 72–78. doi: 10.1016/j.mex.2015.02.008.
- Fageria, N.K. (2007). Yield physiology of rice. *Journal of Plant Nutrition*, doi: 10.1080/15226510701374831.
- Filgueiras, L. et al. (2020). *Gluconacetobacter diazotrophicus* mitigates drought stress in *Oryza sativa* L. *Plant and Soil*, 451(1–2), 57–73. doi: 10.1007/s11104-019-04163-1.
- Flowers, T.J. (2004). Improving crop salt tolerance. *Journal of Experimental Botany*, 55(396), 307–319. doi: 10.1093/jxb/erh003.
- Gimenez-Ibanez, S., Chini, A. and Solano, R. (2016). How microbes twist jasmonate signaling around their little fingers. *Plants*, 5(1), 323–329. doi: 10.3390/plants5010009.
- Glick, B.R. (2014). Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiological Research*, 169(1), 30–39. doi: 10.1016/j.micres.2013.09.009.
- Goswami, M. and Deka, S. (2020). Plant growth-promoting rhizobacteria—alleviators of abiotic stresses in soil: A review. *Pedosphere*, 30(1), 40–61. doi: 10.1016/S1002-0160(19)60839-8.
- Gouda, S. et al. (2018). Revitalization of plant growth promoting rhizobacteria for sustainable development in agriculture. *Microbiological Research*, 206(October 2017), 131–140. doi: 10.1016/j.micres.2017.08.016.
- Govindarajan, M. et al. (2008). Effects of the inoculation of *Burkholderia vietnamensis* and related endophytic diazotrophic bacteria on grain yield of rice. *Microbial Ecology*, 55(1), 21–37. doi: 10.1007/s00248-007-9247-9.
- Grover, M. et al. (2011). Role of microorganisms in adaptation of agriculture crops to abiotic stresses. *World Journal of Microbiology and Biotechnology*, 27(5), 1231–1240. doi: 10.1007/s11274-010-0572-7.
- Gupta, D. et al. (2020). Research Paper production of salicylic acid by a purple non sulfur bacterium *rubrivivax gelatinosus* strain rasn4 from. 09(1), 6718–6736.
- Gyaneshwar, P. et al. (2002). Role of soil microorganisms in improving P nutrition of plants. *Plant and Soil*, 245(1), 83–93. doi: 10.1023/A:1020663916259.
- Habibi, S. et al. (2019). Isolation and screening of indigenous plant growth-promoting rhizobacteria from different rice cultivars in afghanistan soils. *Microbes and Environments*, 34(4), 347–355. doi: 10.1264/j sme2.ME18168.
- Holland, M.A. (1997). Occam's razor applied to hormonology: Are cytokinins produced by plants?. *Plant Physiology*, 115(3), 865–868. doi: 10.1104/pp.115.3.865.

- Ilangumaran, G. and Smith, D.L. (2017). Plant growth promoting rhizobacteria in amelioration of salinity stress: A systems biology perspective. *Frontiers in Plant Science*, 8, 1–14. doi: 10.3389/fpls.2017.01768.
- Imchen, M. et al. (2019). 16S rRNA gene amplicon based metagenomic signatures of rhizobiome community in rice field during various growth stages. *Frontiers in Microbiology*, 10, 1–15. doi: 10.3389/fmicb.2019.02103.
- James, E.K. et al. (2002). Infection and colonization of rice seedlings by the plant growth-promoting bacterium *Herbaspirillum seropedicae* Z67. *Molecular Plant-Microbe Interactions*, 15(9), 894–906. doi: 10.1094/MPMI.2002.15.9.894.
- Jha, P.N. et al. (2020). Alterations in the endophyte-enriched root-associated microbiome of rice receiving growth-promoting treatments of urea fertilizer and rhizobium biofertilizer. *Microbial Ecology*, 79(2), 367–382. doi: 10.1007/s00248-019-01406-7.
- Kakar, K.U. et al. (2016). A consortium of rhizobacterial strains and biochemical growth elicitors improve cold and drought stress tolerance in rice (*Oryza sativa* L.). *Plant Biology*, 18(3), 471–483. doi: 10.1111/plb.12427.
- Kandaswamy, R. et al. (2019). Impact of *Pseudomonas putida* RRF3 on the root transcriptome of rice plants: Insights into defense response, secondary metabolism and root exudation. *Journal of Biosciences*, 44(4), 1–13. doi: 10.1007/s12038-019-9922-2.
- Karadeniz, A., Topcuo S.F. and Inan, S. (2006). Auxin, gibberellin, cytokinin and abscisic acid production in some bacteria. *World Journal of Microbiology and Biotechnology*, 22(10), 1061–1064. doi: 10.1007/s11274-005-4561-1.
- Karnwal, A. and Kaushik, P. (2011). Cytokinin production by fluorescent *Pseudomonas* in the presence of rice root exudates. *Archives of Phytopathology and Plant Protection*, 44(17), 1728–1735. doi: 10.1080/03235408.2010.526768.
- Kasim, W.A. et al. (2013). Control of drought stress in wheat using plant-growth-promoting bacteria. *Journal of Plant Growth Regulation*, 32(1), 122–130. doi: 10.1007/s00344-012-9283-7.
- Kazemi-Shahandashti, S.S. and Maali-Amiri, R. (2018). Global insights of protein responses to cold stress in plants: Signaling, defence, and degradation. *Journal of Plant Physiology*, 226, 123–135. doi: 10.1016/j.jplph.2018.03.022.
- Khan, M.M.A. et al. (2017). Enhancement of growth and grain yield of rice in nutrient deficient soils by rice probiotic bacteria. *Rice Science*, 24(5), 264–273. doi: 10.1016/j.rsci.2017.02.002.
- Knief, C. et al. (2012). Metaproteogenomic analysis of microbial communities in the phyllosphere and rhizosphere of rice. *ISME Journal*, 6(7), 1378–1390. doi: 10.1038/ismej.2011.192.
- Krithika, S. and Balachandar, D. (2016). Expression of zinc transporter genes in rice as influenced by zinc-solubilizing enterobacter cloacae strain ZSB14. *Frontiers in Plant Science*, 7(APR2016), 1–9. doi: 10.3389/fpls.2016.00446.
- Kumar, A. et al. (2015). Does a plant growth promoting rhizobacteria enhance agricultural sustainability?. *Journal of Pure and Applied Microbiology*, 9(1), 715–724.
- Kumar, R.R. et al. (2019). RuBisCo activase—a catalytic chaperone involved in modulating the RuBisCo activity and heat stress-tolerance in wheat. *Journal of Plant Biochemistry and Biotechnology*, 28(1), 63–75. doi: 10.1007/s13562-018-0463-9.
- Lata, R. et al. (2018). Induction of abiotic stress tolerance in plants by endophytic microbes. *Letters in Applied Microbiology*, 66(4), 268–276. doi: 10.1111/lam.12855.
- Lee, H.S. et al. (2006). Physiological enhancement of early growth of rice seedlings (*Oryza sativa* L.) by production of phytohormone of N₂-fixing methylotrophic isolates. *Biology and Fertility of Soils*, 42(5), 402–408. doi: 10.1007/s00374-006-0083-8.
- Li, P. et al. (2019). Identification and characterization of the first cytokinin glycosyltransferase from rice. *Rice*, 12(1). doi: 10.1186/s12284-019-0279-9.

- Li, X. et al. (2018). Exogenous melatonin alleviates cold stress by promoting antioxidant defense and redox homeostasis in camellia sinensis L. *Molecules*, 23(1). doi: 10.3390/molecules23010165.
- Liu, K. et al. (2018). Mixtures of plant-growth-promoting rhizobacteria enhance biological control of multiple plant diseases and plant-growth promotion in the presence of pathogens. *Plant Disease*, 102(1), 67–72. doi: 10.1094/PDIS-04-17-0478-RE.
- Loaces, I., Ferrando, L. and Scavino, A.F. (2011). Dynamics, diversity and function of endophytic siderophore-producing bacteria in rice. *Microbial Ecology*, 61(3), 606–618. doi: 10.1007/s00248-010-9780-9.
- Lucas, J.A. et al. (2014). Beneficial rhizobacteria from rice rhizosphere confers high protection against biotic and abiotic stress inducing systemic resistance in rice seedlings. *Plant Physiology and Biochemistry*, 82, 44–53. doi: 10.1016/j.plaphy.2014.05.007.
- Malukani, K.K. et al. (2019). Induction and suppression of rice innate immunity. *Indian Journal of Genetics and Plant Breeding (The)*, 79(01S), 171–180. doi: 10.31742/ijgpb.79s.1.6.
- Meyer, J.M. (2000). Proverdines: Pigments, siderophores and potential taxonomic markers of fluorescent pseudomonas species. *Archives of Microbiology*, 174(3), 135–142. doi: 10.1007/s002030000188.
- Mishra, R.C. and Grover, A. (2016). ClpB/Hsp100 proteins and heat stress tolerance in plants. *Critical Reviews in Biotechnology*, 36(5), 862–874. doi: 10.3109/07388551.2015.1051942.
- Mohammadipanah, F. and Zamanzadeh, M. (2019). Bacterial mechanisms promoting the tolerance to drought stress in plants, Secondary Metabolites of Plant Growth Promoting Rhizomicroorganisms: Discovery and Applications. doi: 10.1007/978-981-13-5862-3_10.
- Moronta-Barrios, F. et al. (2018). Bacterial microbiota of rice roots: 16s-based taxonomic profiling of endophytic and rhizospheric diversity, endophytes isolation and simplified endophytic community. *Microorganisms*, 6(1), 14. doi: 10.3390/microorganisms6010014.
- Nandakumar, R. et al. (2001). A new bio-formulation containing plant growth promoting rhizobacterial mixture for the management of sheath blight and enhanced grain yield in rice. 493–510.
- Narayanasamy, S., Thangappan, S. and Uthandi, S. (2020). Plant growth-promoting bacillus sp. cahoots moisture stress alleviation in rice genotypes by triggering antioxidant defense system. *Microbiological Research*, 239. doi: 10.1016/j.micres.2020.126518.
- Nasarudin, N.A. et al. (2018). Effect of nitrogen, phosphorus and potassium (nPK) and bacterial bio-fertilizer on the antioxidant activity and chlorophyll content of aerobic rice. *Molecules*, 23(55), 1–9. doi: 10.3390/molecules23010055.
- Nascimento, F.X., Rossi, M.J. and Glick, B.R. (2018). Ethylene and 1-aminocyclopropane-1-carboxylate (ACC) in plant–bacterial interactions. *Frontiers in Plant Science*, 9, 1–17. doi: 10.3389/fpls.2018.00114.
- Orozco-Mosqueda, M. del C. et al. (2018). Microbiome engineering to improve biocontrol and plant growth-promoting mechanisms. *Microbiological Research*, 208, 25–31. doi: 10.1016/j.micres.2018.01.005.
- Panhwar, Q.A. et al. (2011). Role of phosphate solubilizing bacteria on rock phosphate solubility and growth of aerobic rice. *Journal of Environmental Biology*, 32(5), 607–612.
- Panhwar, Q.A. et al. (2014). Biochemical and molecular characterization of potential phosphate-solubilizing bacteria in acid sulfate soils and their beneficial effects on rice growth. *PLoS ONE*, 9(10). doi: 10.1371/journal.pone.0116035.
- Patel, S., Sayyed, R.Z. and Saraf, M. (2016). Bacterial determinants and plant defense induction: Their role as biocontrol agents in sustainable agriculture. *Plant, Soil and Microbes: Volume 2: Mechanisms and Molecular Interactions*, 187–204. doi: 10.1007/978-3-319-29573-2_9.
- Persello-Cartieaux, F. et al. (2001). Utilization of mutants to analyze the interaction between *Arabidopsis thaliana* and its naturally root-associated *Pseudomonas*. *Planta*, 212(2), 190–198. doi: 10.1007/s004250000384.

- Pieterse, C.M.J. et al. (2001). Rhizobacteria-mediated induced systemic resistance: Triggering, signalling and expression. *European Journal of Plant Pathology*, 107(1), 51–61. doi: 10.1023/A:1008747926678.
- Raaijmakers, J.M. and Mazzola, M. (2012). Diversity and natural functions of antibiotics produced by beneficial and plant pathogenic bacteria. *Annu Rev Phytopathol.*, 50, 403-424. doi: 10.1146/annurev-phyto-081211-172908.
- Rais, A. et al. (2016). Plant growth promoting rhizobacteria suppress blast disease caused by *Pyricularia oryzae* and increase grain yield of rice. *BioControl*, 61(6), 769–780. doi: 10.1007/s10526-016-9763-y.
- Raja, P. et al. (2006). Impact of bio inoculants consortium on rice root exudates, biological nitrogen fixation and plant growth. *Journal of Biological Sciences*, 815–823. doi: 10.3923/jbs.2006.815.823.
- Redman, R.S. et al. (1999). Biochemical analysis of plant protection afforded by a nonpathogenic endophytic mutant of *Colletotrichum magna*. *Plant Physiology*, 119(2), 795–804. doi: 10.1104/pp.119.2.795.
- Rekha, K., Ramasamy, M. and Usha, B. (2020). Root exudation of organic acids as affected by plant growth-promoting rhizobacteria *Bacillus subtilis* RR4 in rice. *Journal of Crop Improvement*, 34(4), 571–586. doi: 10.1080/15427528.2020.1746719.
- Rima, F.S. et al. (2018). Bacteria endemic to saline coastal belt and their ability to mitigate the effects of salt stress on rice growth and yields. *Annals of Microbiology*, 68(9). doi: 10.1007/s13213-018-1358-7.
- Rungin, S. et al. (2012). Plant growth enhancing effects by a siderophore-producing endophytic streptomycete isolated from a Thai jasmine rice plant (*Oryza sativa* L. cv. KDML105). *Antonie van Leeuwenhoek, International Journal of General and Molecular Microbiology*, 102(3), 463–472. doi: 10.1007/s10482-012-9778-z.
- Saha, M. et al. (2016). Microbial siderophores and their potential applications: a review. *Environmental Science and Pollution Research*, 23(5), 3984–3999. doi: 10.1007/s11356-015-4294-0.
- Sahoo, R.K. et al. (2014). Phenotypic and molecular characterization of native *Azospirillum* strains from rice fields to improve crop productivity. *Protoplasma*, 251(4), 943–953. doi: 10.1007/s00709-013-0607-7.
- Saikia, J. et al. (2018). Alleviation of drought stress in pulse crops with ACC deaminase producing rhizobacteria isolated from acidic soil of Northeast India. *Scientific Reports*, 8(1). doi: 10.1038/s41598-018-21921-w.
- Santos-Medellín, C. et al. (2017). Drought stress results in a compartment-specific restructuring of *mBio*, 8(4: 8:e00764-17), 1–15. doi: 10.1128/mBio.00764-17.
- Sarkar, A. et al. (2018). A halotolerant enterobacter sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Research in Microbiology*, 169(1), 20–32. doi: 10.1016/j.resmic.2017.08.005.
- Schulz, B. et al. (2002). Endophytic fungi: A source of novel biologically active secondary metabolites. *Mycological Research*, 106(9), 996–1004. doi: 10.1017/S0953756202006342.
- Shahzad, R. et al. (2017). Inoculation of abscisic acid-producing endophytic bacteria enhances salinity stress tolerance in *Oryza sativa*. *Environmental and Experimental Botany*, 136, 68–77. doi: 10.1016/j.envexpbot.2017.01.010.
- Shakeel, M. et al. (2015). Root associated *Bacillus* sp. improves growth, yield and zinc translocation for basmati rice (*Oryza sativa*) varieties. *Frontiers in Microbiology*, 6. doi: 10.3389/fmicb.2015.01286.
- Sharma, A. et al. (2015). Evaluation of different PGPR strains for yield enhancement and higher zn content in different genotypes of rice (*Oryza Sativa* L.). *Journal of Plant Nutrition*, 38(3), 456–472. doi: 10.1080/01904167.2014.934475.
- Sharma, A. and Johri, B.N. (2003). Growth promoting influence of siderophore-producing *Pseudomonas* strains GRP3A and PRS9 in maize (*Zea mays* L.) under iron limiting conditions. *Microbiological Research*, 158(3), 243–248. doi: 10.1078/0944-5013-00197.
- Singh, A. et al. (2016). Impact of addition of biochar along with PGPR on rice yield, availability of nutrients and their uptake in alluvial soil. *Journal of Pure and Applied Microbiology*, 10(3), 2181-2188.
- Singh, R.K., Malik, N. and Singh, S. (2013). Improved nutrient use efficiency increases plant growth of rice with the Use of IAA-Overproducing strains of endophytic burkholderia cepacia Strain RRE25. *Microbial Ecology*, 66(2), 375–384. doi: 10.1007/s00248-013-0231-2.

- Souza, R. De et al. (2013). The effect of plant growth-promoting rhizobacteria on the growth of rice (*Oryza sativa* L.) cropped in southern Brazilian fields. 32, 585–603. doi: 10.1007/s11104-012-1430-1.
- Spoel, S.H. and Dong, X. (2012). How do plants achieve immunity? Defence without specialized immune cells. *Nature Reviews Immunology*, 12(2), 89–100. doi: 10.1038/nri3141.
- Srivastava, Suchi et al. (2016). Unraveling aspects of *Bacillus amyloliquefaciens* mediated enhanced production of rice under biotic stress of *Rhizoctonia solani*. *Frontiers in Plant Science*, 7(MAY2016), 1–16. doi: 10.3389/fpls.2016.00587.
- Steffens, B. (2014). The role of ethylene and ROS in salinity, heavy metal, and flooding responses in rice. *Frontiers in Plant Science*, 5(DEC), 1–5. doi: 10.3389/fpls.2014.00685.
- Sun, L. et al. (2020). The endophyte *Pantoea alhagi* nx-11 alleviates salt stress damage to rice seedlings by secreting exopolysaccharides. *Frontiers in Microbiology*, 10. doi: 10.3389/fmicb.2019.03112.
- Tariq, M. et al. (2007). Plant root associated bacteria for zinc mobilization in rice. *Pakistan Journal of Botany*, 39(1), 245–253.
- Tariq, M. et al. (2017). Características antagónicas que muestran las rizobacterias promotoras de crecimiento de plantas (PGPR): una revisión. *Journal of Plant*, 38–43.
- Tkacz, A. and Poole, P. (2015). Role of root microbiota in plant productivity. *Journal of Experimental Botany*, 66(8), 2167–2175. doi: 10.1093/jxb/erv157.
- Vaid, S.K. et al. (2014). Effect of zinc solubilizing bacteria on growth promotion and zinc nutrition of rice. *Journal of Soil Science and Plant Nutrition*, 14(4), 889–910. doi: 10.4067/s0718-95162014005000071.
- Van Loon, L.C., Bakker, P.A.H.M. and Pieterse, C.M.J. (1998). Systemic resistance induced by rhizosphere bacteria. *Annual Review of Phytopathology*, 36, 453–483. doi: 10.1146/annurev.phyto.36.1.453.
- Vurukonda, S.S.K.P. et al. (2016). Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiological Research*, 184, 13–24. doi: 10.1016/j.micres.2015.12.003.
- Walitang, D.I. et al. (2017). Characterizing endophytic competence and plant growth promotion of bacterial endophytes inhabiting the seed endosphere of rice. *BMC Microbiology*, 17(1), 1–13. doi: 10.1186/s12866-017-1117-0.
- Wang, W. et al. (2016). Endophytic bacterial and fungal microbiota in sprouts, roots and stems of rice (*Oryza sativa* L.). *Microbiological Research*, 188–189, 1–8. doi: 10.1016/j.micres.2016.04.009.
- Wang, W. et al. (2019). Succession of composition and function of soil bacterial communities during key rice growth stages. *Frontiers in Microbiology*, 10, 421. doi: 10.3389/fmicb.2019.00421.
- Wu, Z. et al. (2018). Environmental factors shaping the diversity of bacterial communities that promote rice production. *BMC Microbiology*, 18(1), 1–11. doi: 10.1186/s12866-018-1174-z.
- Yang, Y.X. et al. (2015). Send Orders for reprints to reprints@benthamscience.ae crosstalk among jasmonate, salicylate and ethylene signaling pathways in plant disease and immune responses. *Current Protein and Peptide Science*, 16, 450–461.
- Yanni, Y.G. and Dazzo, F. B. (2010). Enhancement of rice production using endophytic strains of *Rhizobium leguminosarum* bv. *trifolii* in extensive field inoculation trials within the Egypt Nile delta. 129–142. doi: 10.1007/s11104-010-0454-7.
- Ye, N., Jia, L. and Zhang, J. (2012). ABA signal in rice under stress conditions. *Rice*, 5(1), 1–9. doi: 10.1186/1939-8433-5-1.
- Yin, C.C. et al. (2017). Diverse roles of ethylene in regulating agronomic traits in rice. *Frontiers in Plant Science*, 8(September), 1–12. doi: 10.3389/fpls.2017.01676.
- Yoo, S.J. et al. (2019). Induced tolerance to salinity stress by halotolerant bacteria *Bacillus aryabhatai* H19-1 and *B. mesonae* H20-5 in tomato plants. *Journal of Microbiology and Biotechnology*, 29(7), 1124–1136. doi: 10.4014/jmb.1904.04026.

- Zhang, H. et al. (2008). Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. *21(6)*, 737–744.
- Zhang, S. et al. (2002). The role of salicylic acid in induced systemic resistance elicited by plant growth-promoting rhizobacteria against blue mold of tobacco. *Biological Control*, 25(3), 288–296. doi: 10.1016/S1049-9644(02)00108-1.
- Zhou, Y. et al. (2019). Ethylene biosynthesis, signaling, and crosstalk with other hormones in rice. *Small Methods*, 1900278, 1–20. doi: 10.1002/smt.201900278.

Cite this article as: Protup Kumer Sarker, Dola Karmoker and Anik Kumar Saha (2022). Bacterial associations with rice plants: Their diversity, abundance and importance in rice life cycle. *African Journal of Biological Sciences*. 4(2), 1-18. doi: 10.33472/AFJBS.4.2.2022.1-18.