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Insight of Mechanism of Action of Plant Growth Promoting Rhizobia in Leguminous Crops: A Review

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ABSTRACT

World demand for food supply is burgeoning day by day and the need of the hour is to escalate yield per unit area per unit time. Nevertheless, to meet such enormous demand for food, inclination toward inorganic fertilizers has bolstered. It would not only be exorbitant but could grievously degrade the environment through climate change or via contamination of water bodies. There is a need to look for surrogate tactics for climate-resilient agriculture. The microorganisms particularly those that reside in the rhizosphere can play a pertinent role in ameliorating yield without having any detrimental effect on the environment. These organisms are called plant growth-promoting rhizobacteria (PGPR); these can be ePGPR or iPGPR depending on their location whether inside the host plant or outside the host plant. Further, Plant growth promoting rhizobia can play a significant role in improving soil health and enhancing yield through their symbiotic association with legume plants via biological nitrogen fixation (BNF), phosphate solubilization, phytohormone production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity or siderophore production. In the neoteric era, a myriad liquid or charcoal carrier-based formulations of PGPR as microbial inoculants are accessible in the market. However, liquid formulations of microbial inoculants have specific advantages over charcoal-based formulations. Furthermore, dual inoculation or amalgamation of microbial inoculants has a synergistic effect on individuals in crop production. Wherefore, this review will provide a concise account of legume-rhizobial symbiosis, various mechanisms of action of microbes associated with legumes in addition to BNF, the benefits of liquid microbial inoculants and the significance of co-inoculation of symbiotic and other microbial inoculants. The realization attained from the present review herein will further help the fellow scientist to conceive better research ideas keeping in view the multifaceted characteristics of rhizobia.

Key words: Legumes, Microbial inoculants, Rhizobia, Symbiosis.

Global food demand is projected to double in the next 50 years and to feed the burgeoning world population, unprecedented agricultural intensification and improved crop yield will be essential (Fox *et al.,* 2007). Numerous species of soil bacteria flourish in the rhizosphere of plants, grow in, on, or around plant tissues, stimulating plant growth by a plethora of mechanisms. These bacteria are collectively known as PGPR (plant growth promoting rhizobacteria) (Vessey, 2003). These can be separated into extracellular (ePGPR), existing in the rhizosphere, on the rhizoplane, or in the spaces between cells of the root cortex and intracellular (iPGPR), which exist inside root cells, generally in specialized nodular structures (Figueiredo *et al*. 2011). Some examples of ePGPR are *Agrobacterium, Arthrobacter, Azoto bacter, Azospirillum, Bacillus, Burkholderia*, *Caulobacter, Chromobacterium, Erwinia, Flavobacterium, Micrococcus, Pseudomonas* and *Serratia, etc* (Bhatta charyya and Jha, 2012). Similarly, some examples of iPGPR are *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium* and *Rhizobium* of the family Rhizobiaceae. Most the rhizo bacteria belonging to this group are Gram-negative rods with a lower proportion being Gram-positive rods, cocci, or pleomorphic (Bhattacharyya and Jha, 2012). Microbial inoculants play a crucial role in integrated nutrient management and are an eco-friendly, economical and renewable source of plant nutrients (Ramya and Pandove, 2019).

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Further, Plant growth promoting rhizobacteria promotes the growth of plants by multifarious direct and indirect mechanisms such as nitrogen fixation, phosphate solubilization, phytohormones production (IAA, cytokinins, gibberellins), HCN production, siderophore production and ACC-deaminase activity.

Similarly, some *Rhizobium* strains also take part in PGPR activity in addition to biological nitrogen fixation (Deshwal *et al*., 2003). Rhizobia can improve the growth of the plant in a variety of ways such as ACC (1-amino cyclopropane-1-carboxylate) deaminase production, nitrogen fixation, IAA and siderophore production, solubilization of potassium, zinc and organic and inorganic phosphate (Ahmad *et al.,* 2013). Ahemad and Khan (2012) also reported the production of IAA by most Rhizobium species. Yanni *et al.* (2001) also reported that *Rhizobium* strains produce indole 3-acetic acid and GA7 tentatively from their pure culture. Likewise, a few strains or species of *Rhizobium* are involved in phosphate solubilization as reported by Deshwal *et al.* (2003). A great number of observations on rhizobial diversity have been examined and numerous new rhizobial species have been reported, including rhizobia with plant growth-promoting features (PGPB) (Wrobel *et al.,* 2017). Thus, legumes are the well-appreciated builders and curators of soil fertility, primarily through their association with symbiotic nitrogen fixation (Gopala krishnan *et al*., 2014). Pandove and Singh (2019) also believed that sustainable agricultural production requires new approaches to reduce the application of polluting agrochemicals.

Thereupon, the present review will feature legume-rhizobial symbiosis, various mechanisms of action of microbes associated with legumes, the benefits of liquid microbial inoculants and significance of co-inoculation of symbiotic and other microbial inoculants.

Legume-rhizobial symbiosis (Fig 1)

Among the plant-microbe interactions, the legume-*Rhizobium* symbiosis forms a stable system where the host plant, gains a constant supply of reduced nitrogen from *Rhizobia* and *Rhizobia* in return are supplied with photosynthates (carbon) and other nutrients by the host plant. The host plant also provides an environment for *Rhizobial* growth and metabolism. *Rhizobia*-legume symbiosis has been reported to supply half of the biological source of fixed nitrogen and is the primary source of fixed nitrogen in land-based systems (Fox *et al.,* 2007). It is a good option for rotation with cereals as it supplements the soil with nitrogen. Besides improving fertility, it helps in restoring organic matter, smothering weeds, improving the soil's physical environment, solubilizing insoluble phosphorus in the soil and increasing soil microbial activity (Ghosh *et al.,* 2007). The competence of the legumes to form symbiotic associations with a wide choice of *rhizobia* species is referred to as promiscuity. Examples of promiscuous legumes include cowpea, siratro [*Macroptilium atropurpureum* (DC.) Urb.] and common bean (*Phaseolus vulgaris* L.). *Rhizobium* legume symbiosis is the initial source of fixed nitrogen that boosts the biological nitrogen fixation into the soil environment through nodule formation. The formation of these unique plant structures called nodules is the outcome of a three-step process: pre-infection, infection and nodule development. Between the host plant and the free-living *rhizobium*, an exchange of chemical signals occurs before infection. Plant signals induce *nod* genes in *rhizobia* that lead to the synthesis of Nod factors such as lipo-polysaccharides, exopolysaccharides, lipo-chitooligo saccharides andcapsular polysaccharides as well as cyclic â-glucans which stimulate the formation of a nodule primordium and infection threads (Batut *et al.,* 2011). Further during the infection process, infection threads originating in the root hairs guide rhizobia to the nodule primordium formed from root cortical cells. Inside the developed nodule the bacterial cell gets surrounded by the host membrane or symbiosome and differentiates into bacteroids. These bacteroids fix atmospheric nitrogen and the symbiosome membrane facilitates the exchange of fixed nitrogen for carbohydrates from the host (Ivanov *et al.,* 2012). Another mode of root infection by rhizobia is through cracks in the epidermis which results from the emergence of lateral roots (Olroyd and Downie., 2008). In this mode of infection, rhizobia gain access to the cortical cells through infection threads originating from the infected epidermal cracks.

Various mechanisms of action of microbial inoculants (Fig 2)

Biological nitrogen fixation

Biological nitrogen fixation (BNF) is the process in which numerous species of bacteria use the enzyme nitrogenase to convert atmospheric Nitrogen into ammonia and nitrate (a form of nitrogen (N) that can then be incorporated into organic components of the bacteria and associated plants) (Unkovich *et al*., 2008). Examples of nitrogen-fixing organisms include cyanobacteria, free-living soil bacteria, such as *Azotobacter and Klebsiella*, bacteria that form associative relationships with plants, *Frankia, Azospirillum*, that form symbiosis with *actinorhizal* plants and*rhizobium* that form symbiotic associations with legumes and *Parasponia* species. Biological nitrogen fixation imparts 180 $\times$ 10^6 metric tons of nitrogen (N) per year globally; out of which symbiotic nitrogen fixation

Fig 1: Nodules of rhizobia, the nitrogen-fixing bacteria on the roots of groundnut. In the symbiotic relationship bacteria fixes, atmospheric nitrogen for the host plants and the host plants provide carbon compounds generated through photosynthesis, as well as a protected niche for the bacteria.

contributes 80% N and the leftover comes from free-living nitrogen fixation.

Fening and Danso (2002) reported that biological nitrogen fixation is determined by the interaction between cowpea genotypes and *rhizobial* strains. Likewise, the numbers and effectiveness of the native *rhizobia* vary from one locality to another. However, it can be adjusted through inoculant application which introduces a specific number of *rhizobia* into the rhizosphere for symbiosis (Keyser and Li 1992). Herridge (2008) reported that grain legumes add more than 20 million tons of fixed nitrogen every year indicating that the contributions of biological nitrogen fixation (BNF) cannot be challenged. Hence, the BNF ability of legumes is a crucial process for sustaining cropland management. Under favorable conditions, biological nitrogen fixation (BNF) by legume crops like cowpea in cropping systems has been considered one of the reasonable options to increase soil nitrogen levels, but also soil productivity (Pule-Meulenberg *et al.,* 2010). Vesterager *et al.* (2008) reported that cowpea fixed around 60% of its nitrogen from the atmosphere amounting to 70 kg nitrogen per ha under sole cropping and 36 kg nitrogen per ha when intercropped with maize in the semi-arid zone of Tanzania. Tahir *et al*., (2009) studied the BNF capacity in cowpea (legume) as of being vital importance to the livelihoods of millions of people in the semi-arid regions of Africa. Studies by Abaidoo *et al*. (2007) demonstrated that different cowpea varieties showed synergistic relationships among inoculated plots with *Rhizobium* strain over uninoculated for the uptake of high nitrogen. Research reports on soybean under field conditions using Brady*rhizobium* inoculation also confirmed the significant positive effect on nitrogen uptake (Tahir *et al*. 2009). The use of *Rhizobial* inoculants in N-depleted smallholder fields has shown the potential to reduce dependence on inorganic Nitrogen. Nawalde and Bhalerao (2015) observed significant improvement in the number and breadth of leaves, height, shoot length androot length of black gram (*Vigna mungo*) with the application of *Rhizobium japonicum*. Fernandes and Bhalerao (2015) also executed treatment of mungbean (*Vigna radiata*) seeds with *Azotobacter spp* slurry and observed higher chlorophyll, carbohydrate and protein content of inoculated plants than uninoculated ones.

Indole acetic acid

The best-characterized and physiologically most active auxins (phytohormone) is Indole-3-acetic acid (IAA), which has great physiological effects on plants (Davies, 2010). It plays a pertinent role in many plant activities like the formation of the leaf, development of the embryo, initiation

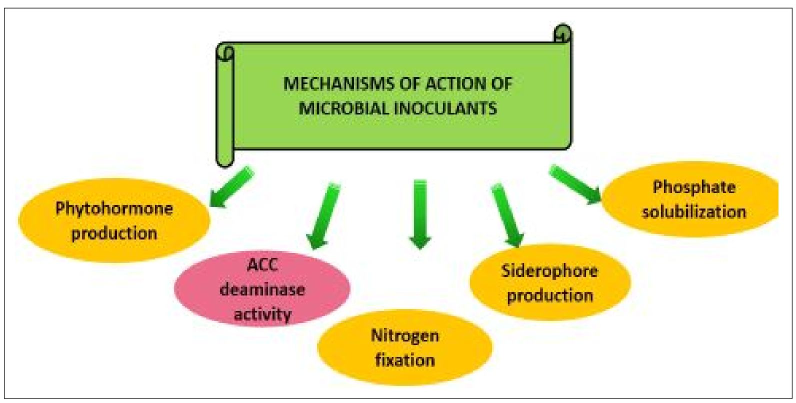

Fig 2: Various mechanisms of action of microbial inoculants.

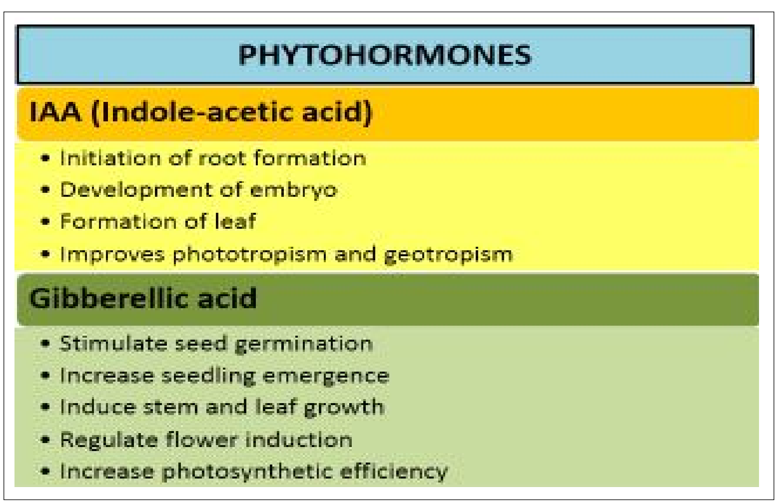

Fig 3: Various important functions of phytohormones.

of root and development, abscission, phototropism, geotropism, *etc* (Fig 3). Indole acetic acid is a common product of L-tryptophan metabolism produced by several microorganisms including PGPR. There are two pathways for IAA biosynthesis, the tryptophan-independent and tryptophan dependent pathways. Indole acetic acid acts as a signal molecule for plant signal processing, motility, or attachment of bacteria in the root which further results in legume-rhizobium symbiosis (Spaepen *et al.,* 2007). IAA is synthesized by PGPR and commonly affects the root system by improving the size and count of adventitious roots, root ramifications, enabling a larger soil volume to be exploited by the roots. Hence, supplying a large number of nutrients to the plant and benefiting the bacteria with high levels of root exudates (Spaepen *et al.,* 2007).

Several workers reported direct involvement of rhizobial IAA in the plant growth-promotion. IAA production in *rhizobium* takes place *via* indole-3-pyruvic acid and indole-3 -acetic aldehyde pathway. On inoculation of *R. leguminosarum bv. viciae*, a 60-fold increase in IAA was observed in the nodules of vetch roots (Camerini *et al.,* 2008). Desbrosses (2011) found that the root nodules of legume plants contain an appreciable amount of IAA that are involved in the genesis and development of nodules. Bacteria use this phytohormone to interact with plants as part of their colonization strategy, including photostimulation and circumvention of basal plant defense mechanisms (Bhattacharyya and Jha 2012). Ghosh *et al.* (2007) observed the production of IAA by bacteria of the nodule from nodular tryptophan and its implication for nodule development was well documented.

Gibberellic acid

Gibberellic acids are hormones (over 120 types found in plants, fungi andbacteria) that control growth and a wide array of plant developmental processes similar to auxins (Cell division and elongation). Additionally, GAs are involved in the natural process of breaking dormancy during seed germination. GAs cause transcription of the gene coding for the a-amylase enzyme to stimulate the enzyme synthesis (Richards *et al.,* 2001). This enzyme hydrolyzes starch into glucose (used for energy by the seed embryo). Gibberellic acids act throughout the life cycle of plants by influencing a wide range of physiological processes such as fruit growth, light interception, nutrient use efficiency, seedling emergence, stem and leaf growth, flower induction, stimulation of seed germination, seed pericarp growth, root hair abundance, photosynthetic efficiency of plants, leaf area index, promotion of root growth and inhibition of floral bud differentiation in woody angiosperms, regulation of vegetative and reproductive bud dormancy and delay of senescence in many organs of a range of plant species (Fig 3). Thus, it provides a mechanism to regulate the metabolic process as a function of sugar signaling and antioxidative enzymes (Iqbal *et al*., 2011).

Gibberellin also favors root nodule symbiosis. It has been proved that in pea, mutants that are deûcient in GA biosynthesis, nodule formation is aborted and is re-established on the application of exogenous GA, although the addition of huge concentrations of GA no longer restores nodule formation in these mutants. The application of higher concentrations of GA also suppresses nodulation in wild-type plants, suggesting that nodule formation is controlled by the endogenous GA concentration in a very strict way (Ferguson *et al*., 2005)..Production of gibberellins have been reported by *Herbaspirillum seropedicae, Gluconobacter diazotrophics, Bacillus pumilus, Azospirillum, Azotobacter, B. licheniformis and Rhizobia* (Bottini *et al*., 2004). Boiero *et al.* (2007) reported the production of gibberellins from Rhizobium, *S. meliloti*. Yanni *et al.* (2001) also revealed the synthesis of auxin (IAA) and gibberellin by pure cultures of Rhizobium strains.

1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (Fig 4)

When plants are grown under unfavorable conditions, the concentration of ethylene (a phytohormone) increases

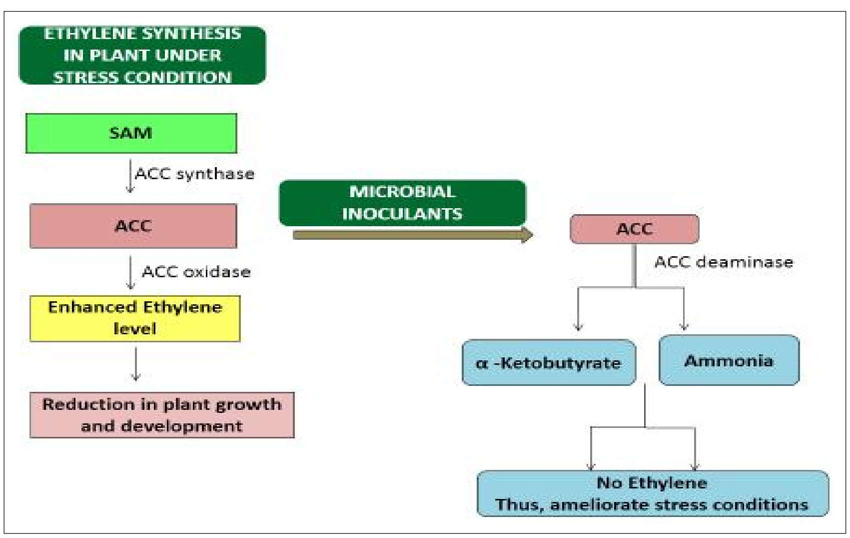

Fig 4: Schematic diagram to explain the ACC deaminase activity of the beneficial bacterial cultures present in microbial inoculants.

significantly and it has a deteriorating effect on the process of nodulation. Thus, a reduction in the concentration of ethylene in the nodulating roots contributes to an enhancement in the nodulation of legumes.

Numerous reports disclosed that ACC deaminase production by rhizobia plays a pertinent role in the symbiotic performance of rhizobia (Conforte *et al.,* 2010). Similarly, exogenous ACC deaminase gene expression in *Sinor hizobium meliloti* enhanced nodulation in alfalfa. Similarly, the ACDS gene of *Mesorhizobium* sp. MAFF 303 099 expresses the ACC deaminase enzyme (Uchiumi *et al*., 2004). Madhaiyan *et al.* (2006) reported that *Rhizobium* strain containing ACC deaminase acts as a sink for 1-amino cyclopropane-1-carboxylate (ACC) by reducing plant ethylene levels, decreasing the inhibiting effect on the growth of roots and declining the gloomy effects of the myriad of environmental stresses (Stearns *et al.,* 2005). Likewise, *Bradyrhizobium japonicum* through the production of ACC deaminase enzyme is able to degrade aminocyclopropane-1-carboxylate (Murset *et al*., 2012).

Phosphate solubilization (Fig 5)

One of the essential macronutrients required for plant growth is phosphorus (P), it has no source in the atmosphere as in the case of nitrogen. Many microorganisms (bacteria, fungi andactinomycetes) found in soil play a fundamental role in the biogeochemical cycling of phosphorus in natural and agricultural ecosystems. The microorganisms having the phosphate solubilizing capacity convert the insoluble phosphates into soluble forms through the production of organic acids (Qureshi *et al*., 2012), chelation and ion exchange (Whitelaw, 2000). Nonetheless, bacteria are most effective in phosphorus solubilization than fungi (Alam *et al*., 2002). A considerably higher concentration of phosphate solubilizing bacteria is commonly found in the rhizosphere in comparison with non-rhizosphere soil (Khalid, 2012). The positive effect of phosphorus solubilizers had been reported on food and fodder crops by several researchers (Dey *et al.,* 2004). Bacterial genera like *Azotobacter, Bacillus, Beijerinckia, Burkholderia, Enterobacter, Erwinia, Flavobacterium, Microbacterium, Pseudomonas, Rhizobium and Serratia* are reported as the most significant phosphate solubilizing bacteria (Bhattacharyya and Jha, 2012). Rhizobia like, including *R. meliloti*, *R. leguminosarum*, *M. medi terraneum*, *Bradyrhizobium* sp. and *B. japonicum* (Afzal and Bano, 2008, Egamberdiyeva *et al*., 2004; Rodrigues *et al*., 2006; Vessey, 2003) are the potential P solubilizers. Peix *et al.* (2015) also reported that phosphate solubilizing bacteria encompasses symbiotic bacteria like *Rhizobium*, *Mesorhizobium*, *Bradyrhizobium* in addition to the free-living forms.

Alikhani *et al*. (2006) isolated considerable rhizobia from Iranian soils with the ability to mobilize inorganic and organic phosphates, it was confirmed by the decrease in pH of the culture filtrate with the release of soluble phosphate which indicates the importance of organic acid production. Kumari *et al*. (2009) reported that besides the acid production believed to be responsible for phosphate solubilization activity of rhizobia, it has been found that rhizobia could produce other factors like exopolysaccharide and indole acetic acid which may also be related to its phosphate solubilization activity of rhizobia. Abbasi *et al.* (2010) also reported that in soybean plants (field grown) inoculation with rhizobium enhances phosphorus use efficiency. Singh *et al.* (2017) revealed that 96 pe rcent of rhizobial isolates out of forty-nine pigeon pea rhizobial isolates from arid and semi-arid zones of Haryana were able to form a significant zone of phosphate solubilization on Pikovskaya's medium plates and P-solubilisation index ranged from 1.2 to 3.7. While Jadhav (2013) reported that 3 isolates out of 10 rhizobial isolates from soybean crop showed phosphate solubilization activity.

Siderophore production

Ferric ion (Fe^{3+}) is a general form of iron found in nature and is slightly soluble. This element is a component of many enzymes such as nitrogenase. PGPR secretes siderophores which are the iron-binding protein of low molecular mass and have a high binding affinity with ferric ions. They form the ferric-siderophore complex and make it unavailable to other organisms, but the producing organisms can utilize these complexes with the help of a specific receptor present

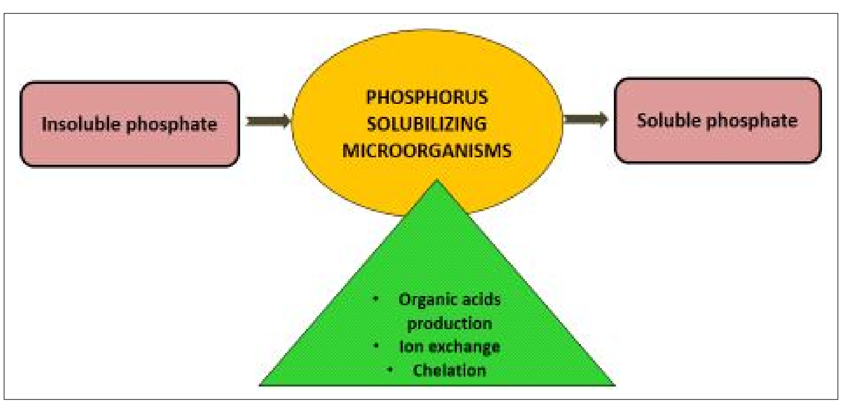

Fig 5: Schematic diagram to explain the phosphate solubilizing activity of beneficial bacteria.

on their outer cell membrane. Thus, due to iron starvation, the growth of pathogenic fungi and bacteria in the rhizosphere gets restricted (Fig 6).

Reigh and O'Connell (1993) reported that there are numerous strains of rhizobia with the potential to produce siderophores such as *Rhizobium meliloti* DM4.Persmark *et al.* (1993) reported that under iron stress *Sinorhizobium meliloti* synthesize and produces rhizobactin a dihydroxamate siderophore whereas Catecholate siderophores are known to be produced by rhizobia from the cowpea (Jadhav and Desai, 1992). Berraho *et al.* (1997) reported that *Rhizobium ciceri* from chickpea nodules produces salicylic acid and dihydroxybenzoic acid. In *Sinorhizobium meliloti* 1021 (Lynch *et al.,* 2001) and *Rhizobium leguminosarum bv. viciae* (Carter *et al*., 2002) genes for siderophore biosynthesis were studied. In both the organisms, the genes for biosynthesis of siderophores were located on plasmids. These were clustered close to the genes encoding their cognate membrane proteins. Raychaudhuri *et al.* (2005) also reported that during symbiosis between root nodule bacteria and leguminous plants, nodule formation needs iron as well as leghaemoglobin and nitrogenase for biological nitrogen fixation.

Liquid microbial inoculants

Microbial inoculants can be applied directly to the soil or by coating onto the seed before sowing. The most common formulations consist of peat, granular, liquid, freeze-dried and pre-inoculated seed. Granular and Liquid inoculant formulations are often used in soil rather than seed. This method of inoculation circumvents the realizable toxic effects of seed exudates and chemicals used to treat seeds. In addition, soil application of inoculants allows for greater inoculation rates (Campos *et al*., 2012). Liquid formulations support high population density of bacteria under varying environmental conditions. Liquid inoculant formulations normally consist of certain compounds which serve as cell protectants in addition to all other constituents of specific nutrient media used for the growth of PGPR in a laboratory (Deaker *et al.,* 2004). Liquid cultures amended with cell protectants not only maintain higher microbial counts but also promote the formation of resting cells (cysts and spores) which offer higher resistance to abiotic stresses, thus increasing the survivability of bacteria. Polysaccharides such as gums, carboxy methyl cellulose and polyalcohol derivatives are commonly used to alter the fluid properties of liquid formulations (Paau 1988). Thangaraju (2006) developed a liquid formulation of *Azospirillum brasilense* amended with trehalose, glycerol and PVP in NFb malate broth and reported 10^8 cells/ml up to 10 months of storage under room temperature. Kaur *et al.* (2018b) developed a liquid formulation of *Azotobacter* sp. and *Streptomyces badius* using 2% PEG in basal medium and found maximum viability even after 180 days as compared to charcoal carrier-based formulation (both at room and refrigerated temperature). In addition, liquid inoculants could play a predominant role in mitigating the abiotic and biotic stresses due to climate change (Kaur *et al*., 2018c).

Trehalose escalates cell tolerance to osmotic pressure, desiccation and temperature stress and stabilizes both cell membranes, enzymes and cell membranes. Moreover, some polymeric additives such as starch, PVA and PVP have polymeric properties. The improvement of survival is analogous to the protective colloid effect where bacteria represent one colloid and the suspension the other (Deaker *et al*., 2004). Julca *et al*. (2012) also reported that the accumulation of trehalose (xeroprotectants) by some microorganisms and some plants enables them to combat extreme abiotic stress such as desiccation.

The advantages of liquid biofertilizers over conventional carrier-based biofertilizers include: no loss of properties due to storage at high temperature up to 45°C; high populations can be maintained for more than 10^9 cells/ ml up to 12 to 24 months; longer shelf life (12- 24 months); no effect of high temperature and no contamination; high export potential; easy to use by the farmers; dosages are 10 times less than carrier-based, quality control protocols are easy and quick (Verma 2011).

Significance of Co-inoculation of symbiotic and other microbial inoculants

Legume crops are vital not only for human and animal consumption but also for the environment as they can be grown in low nutrient environments and water-deficient soil due to their ability to form a symbiosis with both arbuscular mycorrhizal (AM) fungi and nitrogen-fixing *Rhizobium*. Application of more than one microbial inoculant (biofertilizers) is being recommended to meet the nitrogen and phosphorus requirement of plant growth. Such synergistic influence of root-nodulating bacteria and PGPR has been reported for myriad crops which include *Rhizobium leguminosarum* bv.*viciae* strains and fluorescent *Pseudomonas* strains in pea (Kumar *et al*., 2001), *Rhizobium*

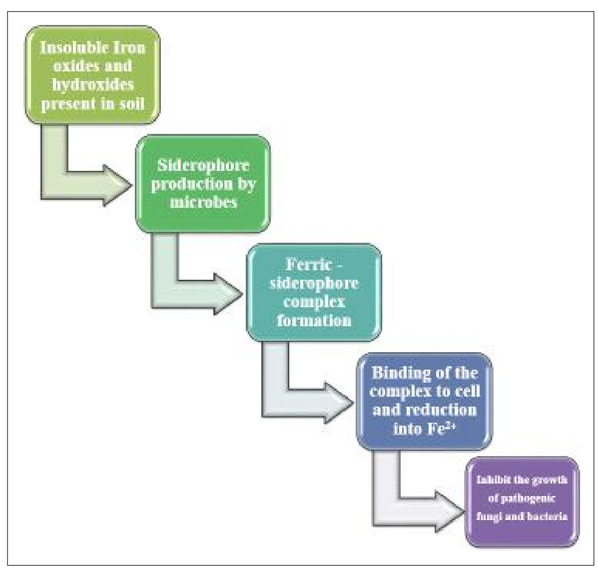

Fig 6: Schematic diagram to explain the activity of siderophores produced by the beneficial bacteria.

leguminosarum bv. *Phaseoli and Pseudomonas* strains in common beans (Martins *et al*., 2003), *Pseudomonas putida* and *P. fluorescens* with *Rhizobium* sp. in pigeon pea (Tilak *et al*., 2005); *Azotobacter chrooo coccum, Mesorhizobium cicero, Pseudomonas*, in chickpea (Wani *et al*., 2007); and *Sinorhizobium meliloti* in alfalfa (Guinazu *et al.,* 2009); *Pseudomonas* spp. and *Rhizobium* in fodder Galega (Egamberdieva *et al*., 2009) and *Bradyrhizobium* plus *Serratia marcescens* in peanut (Badawi *et al*., 2011).

Similarly, Khoja *et al*. (2002) observed that seed inoculation with *Rhizobium* and *PSB* significantly escalated the plant height, the number of branches and dry matter accumulation per plant as well as pods per plant, seeds per pod and test weight, over un-inoculation treatment. Jain and Singh, (2003) demonstrated that seed treatment with *Rhizobium* and PSB showed 8.33%, 24.75% and 13.07% higher plant height, dry matter accumulation and the number of branches/plant of chickpea respectively, over control. Gupta (2004) reported that dual inoculation of *Rhizobium* and phosphate solubilizing bacteria either as seed or as soil inoculation significantly enhanced the nodulation (3.1 to 3.9 times nodule number and 3.2 to 4.2 times nodule dry weight) over control. Chattopadhyay and Datta (2003) studied the effect of biofertilizers on vegetable cowpea and showed that dual inoculation with *Rhizobium* and phosphate-solubilizing bacteria resulted in superior response on yield and nodulation than their single inoculations. Jain and Singh (2003) observed that seed treatment with *Rhizobium* and PSB on sandy clay soil significantly influenced dry matter accumulation, number of branches, plant height and grain yield of chickpea as well as nitrogen and phosphorus contents in grain and their uptake by the crop. Meena *et al.* (2003) reported a significantly higher grain yield of chickpea with PSB inoculation as compared to no inoculation. The total uptake of nitrogen, phosphorus and potassium was also found positively higher in PSB inoculation treatment than in no inoculation. Pathak *et al.* (2003) reported that inoculation of phosphate solubilizing bacteria with 10 tonnes FYM/ha recorded significantly higher plant height, no of branches per plant, root nodulation, pod per plant, full grains per pod which resulted in higher test weight and grain yield of chickpea than other treatments. Tyagi *et al*. (2003) carried out a field experiment to study the dual inoculation impact of *Rhizobium* and phosphate solubilizing bacteria on pea and concluded that the maximum number of nodules, grain and dry matter yield of pea were recorded with collective inoculation of a composite and single culture of *Rhizobium* and PSB. Menariya and Singh (2004) conducted a field experiment to study the effect of chemical and biofertilizers on yield attributing characters, seed and stover yields of soybean. The result revealed that seed inoculation with various inoculants *viz., Bradyrhizobium japonicum* (Rz), phosphate solubilizing bacteria and *Bradyrhizobium japonicum* + PSB significantly improved yield attributes along with seed and stover yields over control.

Zaidi and Khan (2006) evaluated the impacts of nitrogen-fixing (*Bradyrhizobium sp*. (*Vigna*), phosphate solubilizing bacterium (*Bacillus subtilis*) andphosphate solubilizing fungus (*Aspergillus awamori*) on nitrogen and phosphorus uptake of green gram plants and concluded significant improvement in nitrogen and phosphorus uptake by the plant. Yim *et al.* (2009) reported that co-inoculation of *Rhizobia and Pseudomonas* proved to be advantageous to the plant as *Pseudomonas* increases the surface area of roots for attachment of *Rhizobia* or escalates the production and release of flavonoid-like compounds that induce the transcription of rhizobial nodulation genes. Rather *et al.* (2010) studied the effect of the application of biofertilizers (PSB) *Azotobacter*, *Rhizobium* on the growth and yield of field pea (*Pisum sativum* L.) and reported that co-inoculation of all the three bio-fertilizers showed noteworthy improvement in growth characters. Ramana *et al.* (2010) observed that in French beans the application of 75 per cent recommended dose of fertilizer and VAM (Vesicular Arbuscular Mycorrhizae) @ 2 kg ha^{-1} and PSB (Phosphorus Solubilising Bacteria @ 2.5 kg ha^{-1} significantly revamped the plant height (cm), number of branches per plant, leaf area (cm^2) and dry weight (g) of a plant.

According to Tanwar *et al.* (2010) application of Phosphorus (2.58 kg ha^{-1}) along with FYM @ 5 t ha^{-1} and seed inoculation with PSB, results in higher seed (2.86 t ha^{-1}) and stover (8.47 t ha^{-1}) yield in Kabuli chickpea as compared to other treatments with no FYM. Chate *et al.* (2012) observed the application of 150% NPK along with $ZnSO_4$ (25 kg/ha), $FeSO_4$ (25 kg/ha), *Rhizobium* and PSB @ 250 g/10 kg seed resulted in significantly higher grain yield and available nitrogen, phosphorus and potassium(kg/ha). Ahsan *et al.* (2012) demonstrated that phosphate solubilizing bacteria (PSB) and *Bradyrhizobium* had a significant impact on the number of nodules per plant and nodule dry weight per plant of soybean. Sharma *et al.* (2013) also reported that dual inoculation of *Mesorhizobium ciceri* with ACC deaminase producing *Pseudomonas* and *Bacillus* improved germination of seed, the height of shoot, root length of root andfresh weight of seedling in chickpea grown under stressed condition over uninoculated plants. Liquid microbial inoculants could play a predominant role in the integrated nutrient management of forage cowpea for enhanced productivity (Ramya *et al.,* 2020).

Conclusion

Plant growth-promoting rhizobia can play a pertinent role in improving the growth, yield and quality of leguminous crops by the plethora of mechanisms in addition to nitrogen fixation like indole acetic acid production, gibberellic acid production, ACC deaminase activity, phosphate solubilization and siderophore production which have been divulged in this review. Similarly, the application of plant growth-promoting rhizobia in the form of liquid microbial inoculants would further burgeon the growth attributes of the crop due to the improved population density of desired bacteria at the time of application and better field performance. Further, more research work ought to be carried out to develop better inoculants of rhizobia with other potential plant growth-promoting bacteria with the multiplicity of functions to meet the macro and micronutrient requirements of the crops, in addition, to mitigating various biotic and abiotic stress.

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Conflict of interest

The authors disclose that they have no conflict of interest.

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