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MINI-REVIEW

Mechanism and application of *Sesbania* root-nodulating bacteria: an alternative for chemical fertilizers and sustainable development

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Abstract

Chemical fertilizers are used in large-scale throughout the globe to satisfy the food and feed requirement of the world. Demanding cropping with the enhanced application of chemical fertilizers, linked with a decline in the recycling of natural or other waste materials, has led to a decrease in the organic carbon levels in soils, impaired soil physical properties and shrinking soil microbial biodiversity. Sustenance and improvement of soil fertility are fundamental for comprehensive food security and ecological sustainability. To feed the large-scale growing population, the role of biofertilizers and their study tends to be an essential aspect globally. In this review, we have emphasized the nitrogen-fixing plants of *Sesbania* species. It is a plant that is able to accumulate nitrogen-rich biomass and used as a green manure, which help in soil amelioration. Problems of soil infertility due to salinity, alkalinity and waterlogging could be alleviated through the use of biologically fixed nitrogen by *Sesbania* plants leading to the conversion of futile land into a fertile one. A group of plant growth-promoting rhizobacteria termed as "rhizobia" are able to nodulate a variety of legumes including *Sesbania*. The host-specific rhizobial strains can be used as potential alternative for nitrogenous fertilizers as they help the host plant in growth and development and enhance their endurance under stressed conditions. The review gives the depth understanding of how the agriculturally important microorganisms can be used for the reduction of broad-scale application of chemical fertilizers with special attention to *Sesbania*-nodulating rhizobia.

Keywords *Sesbania* · Rhizobia · Chemical fertilizers · Biofertilizer · Microorganisms

Introduction

Application of various chemicals as fertilizers frequently deteriorate soil eco-profile, along with imparting negative influence on the environment and human health, thereby increasing the input cost for crop production especially for the marginal farmers (Bhatt et al. 2019a, 2019b; Gangola et al. 2018; Sharma et al. 2019). These chemicals not only affect soil microbiota but also increase the residue of toxic chemicals at different trophic levels in the food chain (Pankaj et al. 2016a, b). Soil is a vital natural resource decisive for the maintenance of any ecosystem which we need to manage efficiently. Soil is confronting grave threats of declension

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owing to inexorable human pressure and its incompatibility with carrying capacity (Kumar et al. 2019; Bhatt et al. 2020b). There can be significantly severe effects concerning soil erosion, loss of soil fertility, and therefore, decreased plant growth or crop productivity. It is figured that some types of land degradation comprising 75% of the earth's usable landmass influence 4 billion people in the world that constitute around 15% population of the globe which is anticipated to get worse if adequate and instant measures are not taken to check the degradation processes. The maximum degradation occurs due to water and wind erosion, which accounts for 80% of total degradation followed by salinization/alkalization and waterlogging. The hazardous effects of the herbicides, fungicides, insecticides and organic pollutants in agricultural soil depends on their half-life, degradability, adsorption, desorption, bioavailability, bioactivity, persistence, concentration and toxicity of agrochemicals along with soil factors such as texture, vegetation, tillage system and organic matter (Meena et al. 2020). The data on land degradation are required for several purposes such as designing reclamation programs, sound land-use planning, for bringing additional areas into cultivation and also to enhance the productivity levels in degraded lands (Bhatt 2019; Bhatt and Barh 2018). The indigenous microbial strains have the ability to degrade the toxic pesticides from the environment using their metabolic pathways (Bhatt et al. 2020a, b, c, d). Microbial degradation of such toxic chemical fertilizers from the environment is eco-friendly and sustainable approach to resource recovery of the contaminated agricultural fields (Bhatt et al. 2020e, f, g).

Sesbania is a plant of high importance due to the exceptional merit of adapting to a wide range of environments under stress conditions such as salinity, waterlogging and at very high altitudes with high-nitrogen fixation ability. *Sesbania rostrata* has been reported for its role in biological nitrogen fixation and pollution remediation in rice production (Naher et al. 2020). The extent of the diversity of symbiotic nitrogen-fixing bacteria (rhizobia) in the soil is observed to be significant for the conservation of soil health and value, as a broad variety of rhizobia possessing attributes, viz., plant growth promotion (PGP) is involved in important soil functions. Mounting curiosity has arrived with respect to the significance of rhizobia infecting different *Sesbania* species, viz. *S. sesban*, *S. grandiflora*, *S. aculeata* and *S. rostrata* for enhancing plant biomass, which will combat desertification of marginal lands and rehabilitate destructive lands into productive croplands for rigorous crop yield (Fig. 1). They are tremendous nitrogen fixers and adapt quickly in nitrogen poor soils, therefore, have immense usefulness in agroforestry as intercrop, cover crop, green manure, mulch and fodder. Table 1 representing the amount of nitrogen fixed by various legume in crops. Activity and species composition of rhizobia, usually influenced by a number of environmental factors, viz., soil physicochemical properties, temperature as well as vegetation. The research must continue for the legume crops having high nitrogen fixation ability with a beneficial effect on plant and soil health. Swarup (1992) reported the beneficial influence of *Sesbania* spp., as green manure on electrochemical properties and nutrient availability in sodic soils with additional grain yield of 1.48 t ha^{-1}

Fig. 1 Benefits of *Sesbania* plant on soil environment and development of a sustainable environment

Table 1 Amount of nitrogen fixed by different legumes in the soil environment

Crop name	Nitrogen fixed Kg/ha
Alfalfa	229–290
Berseem	130
Black gram	119–140
Chickpea	23–97
Cluster bean	378–196
Cowpea	75–354
Groundnut	25–220
Green gram	50–66
Horse bean	45–552
Leucaena	74–584
Pigeon pea	168–200
Peas	46–77
Mungbean	63–342
Sesbania cannabina	242
Sesbania grandiflora	150–245
Sesbania sesban	250
Sesbania rostrata	310
Soybean	60–168

of rice and 0.66 t ha^{-1} of wheat. To date, different groups of researchers isolated and characterized the rhizobial isolates with *Sesbania* plant. Due to fragmented information, farmers are not able to use these groups of plants and associated bacterial strains for crop improvement. This review increases our understanding of *Sesbania* and associated microbial strains (Fig. 1). The effect of chemical fertilizers can be reduced via using various biofertilizers to recover the agricultural resources. This review throws light on the detailed mechanism of biofertilizers and their application in reduction of chemical fertilizers.

Microbial nitrogen fixation

Following photosynthesis, nitrogen fixation is treated to be another important mechanism to determine the main yield of the crops and is the center of life on earth as nitrogen (N) is essential for the organization of nucleic acids, proteins, enzymes and chlorophyll. It is mainly restrictive and supplied nutrients to nearly all the plants and the decisive of plant development (Puri et al. 2018). The environmental concern is due to the rising quantity of the active mode of nitrogen in the atmosphere, originating from the manufacture and uses of chemical fertilizers have resulted to re-focus on the biological nitrogen fixation (BNF), particularly by legumes (Bhatt et al. 2019c). BNF has been extensively practiced as an alternative of various nitrogen fertilizers in legume production as a consequence of its economic capability in terms of sustainable agroecosystem services. Annually, around 2.5×10^{11} kg NH_3 is fixed from the atmosphere due to BNF (by legumes and Cyanobacteria) and about 8×10^{10} kg NH_3 are manufactured by ammonia industry. Legumes have an advantageous impact on the yield of cereals and alternative crops in agricultural rotations thereby the application of nitrogenous fertilizers is reduced. BNF contributed by the *Rhizobium*-legume association is considered a highly efficient process and may supply up to 90% of the nitrogen requirements for host plants. Hence, the symbiotic association between rhizobia and legume for biological nitrogen fixation is the leading practice because it is environmentally safe and secure. Problems of soil infertility due to salinity, alkalinity and waterlogging could be alleviated through the use of biologically fixed nitrogen by *Sesbania* spp. The current approach comprises the finding of unique rhizobial species, which have an adjustment to numerous abiotic stresses, viz., elevated temperature, drought, alkalinity and salinity. *Sesbania* spp. is well recognized for pursuing a central role in nutrient cycling and nutrient enrichment in various cropping systems. The low productivity in legumes is frequently connected by means of diminishing soil productiveness of the farmland and decreased nitrogen fixation. The yield reduction of legume can be improved through the inoculation of adaptable and effective rhizobia. This practice is constrained mostly to leguminous plants in agricultural systems, thereby generating great curiosity among researchers to examine whether similar symbiosis can be developed in non-legumes as well, delivering maximum food yield for mankind (Mus et al. 2016). Green manuring associated with legumes is an ancient procedure providing biologically fixed N_2 to succeeding crops grown in alternation (Table 2). The rotational profit of legumes and N credit for subsequent cereal crops are extensively known. *Sesbania* is able to fix nitrogen not just via its roots in the soil, but also in its aerial parts together with stems and branches. Rao and Gill (1993) performed large-scale field experiments on *Sesbania* spp. in alkaline soil throughout the summer period (1986, 1987 and 1989) to examine the nodulation, nitrogen fixation, biomass production and uptake of nutrients (N, P, K, Ca, Na, S and Mg). It was observed that natural nutrients (N, P, K, Ca, S and Mg concentrations) uptake in the shoots were towering, while the Na concentration was low, reflecting its usefulness as an integrated biofertilizer source. Hasan et al. (2015) procured 19 rhizobial isolates from *Sesbania* root nodules, from 5 different agro-ecological regions of Bangladesh designated as AEZ 9, AEZ 11, AEZ 12, AEZ 13 and AEZ 28. Rhizobia inoculation on varieties of *Sesbania*, viz., Deshi dhaincha and African dhaincha bear major and assured consequence on the nitrogen content of shoot biomass, shoot parched weight, root parched weight, nodule quantity and nodule parched weight in sterile conditions. Yan et al. (2017)

isolated a Gram-negative, non-spore-forming, aerobic rods strain YIC4121^T, isolated from root nodule of *Sesbania cannabina* grown in Dongying (Yellow River Delta), Shandong Province, PR China. Based on phylogenetic analysis of 16S rRNA gene sequences, strain YIC4121^T was assigned to the genus *Agrobacterium* with 99.7, 99.3, 99.0, 98.8 and 98.7% sequence similarities to *Agrobacterium radiobacter* LMG140^T, *A. pusense* NRCPB10^T, *A. arsenijevicii* KFB 330^T, *A. nepotum* 39/7^T and *A. larrymoorei* ATCC51759^T.

Rhizobial taxonomy and groups of rhizobia infecting *Sesbania* plants

The taxonomy of *Rhizobium* is frequently changing along with the discoveries of newer nodule inhabitants. The currently explained legumes symbionts generally belong to α, β and γ-proteobacteria, the three main phylogenetic subclasses. The genera *Rhizobium*, *Mesorhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Bradyrhizobium*, *Phyllobacterium*, *Microvirga*, *Azorhizobium*, *Ochrobactrum*, *Methylobacterium*, *Devosia*, *Shinella* (Class of α-proteobacteria), *Burkholderia*, *Cupriavidus* (formerly *Ralstonia*) (Class of β-proteobacteria) and some γ-proteobacteria form the set of the bacteria known as legumes symbionts. The advent of new genera and species from nodules of different legumes, currently, rhizobia consist of 118 species belonging to 17 different genera, viz., *Azorhizobium*, *Bradyrhizobium*, *Burkholderia*, *Cupriavidus*, *Devosia*, *Ensifer*, *Herbaspirillum*, *Mesorhizobium*, *Methylobacterium*, *Microvirga*, *Ochrobactrum*, *Phyllobacterium*, *Pseudomonas*, *Ralstonia*, *Rhizobium*, *Shinella* and *Sinorhizobium* (Pongsilp 2017). The recent use of whole-genome sequencing-based taxonomy (genomotaxonomy) will obviously change the current concept of this important group of bacteria. Molecular study on the basis of the 16S ribosomal DNA sequence, presently described legumes symbionts belong to α, β and γ-proteobacteria phylogenetic subclasses, in which 238 species were grouped into 18 genera and 2 clades (Pankaj et al. 2014; Shamseldin et al. 2017).

The compatibility of host and microsymbiont in legume–*Rhizobium* symbiosis is a prerequisite for nodule formation. *Sesbania* nodules may be induced by a variety of rhizobia, including *Azorhizobium* spp., *Ensifer* spp., (syn. *Sinorhizobium* spp.), *Mesorhizobium* spp., and *Rhizobium* spp. In addition to the standard rhizobial types, strains of the genus *Agrobacterium* have also been frequently isolated from *Sesbania* nodules. *Sesbania rostrata* and other *Sesbania* species may also form a symbiosis with other rhizobia (Dreyfus et al. 1988), including the newly described species *Sinorhizobium saheli* and *S. teranga*. The latter species has been subdivided into bv. *Sesbania* (*Sesbania*-nodulating strains) and bv. *Acaciae* (*Acacia*-nodulating strains). The ability of such distantly related bacteria to establish interactions with *Sesbania* species raises the questions whether *Sinorhizobia* exhibit the unusual characteristics of *Azorhizobia*, i.e. stem nodulation and free-living N_2 fixation, or whether they have similar or specific symbiotic properties.

Effect of rhizobial inoculation on nodulation efficiency and plant growth promotion

Increasing production of grain legumes is well recognized as a vital component of sustainable intensification strategies. Legumes capability of converting and thereby fixing atmospheric nitrogen by symbiotic rhizobia offers the potential substitute of nitrogen fertilizers along with enhancing the biological yield of crops. For the establishment of legume root nodules to provide a functioning N_2-fixing symbiosis requires an ample number of root-nodulating bacteria in the soil or to be provided during the course of sowing (Thilakaranthna and Raizada 2017). However, the introduction of rhizobial strain establishment, the persistence, as well as the efficacy, generally decreases with an increase in the population density, perhaps due to the possibility of negative microbial interaction or incompatibility with the other symbionts within the rhizosphere. Therefore, the application of native rhizobial strain serves better as biofertilizers, which would improve soil biodiversity conservation (de Mandal and Bhatt 2020). Bio-fertilization limits the negative effects resulting from the inorganic fertilizers on below-ground biodiversity. Since rhizobia are poorly motile in soils, so the point of delivery of rhizobia into the soil is a determinant of nodulation pattern. Inoculation with compatible and appropriate rhizobia may be necessary, where a low population of native rhizobial strains predominates and is one of the solutions, which can be utilized by the farmers for optimizing grain legume yields. Mondal et al. (2017) observed that inoculation of abiotic stress-tolerant cluster bean rhizobial isolates enhanced 80–90% in nodulation efficiency and plant growth over uninoculated control. Van Heerwaarden et al. (2018) found inoculation response of *Rhizobium* to soybean across sub-Saharan Africa, where the average yields were estimated to be about 1343 (with inoculation) and 1227 $kg \cdot ha^{-1}$ (without inoculation). Li et al. (2019) isolated Strain KG2 from soybean nodule which was identified as *Rhizobium pusense* KG2 by phylogenetic analysis. *Rhizobium pusense* KG2 showed the 120 $mg \cdot L^{-1}$ of minimal lethal concentration for Cd^2. In 50 and 100 $mg \cdot L^{-1}$ of Cd^{2+} liquid, approximately 2×10^{10} cells removed 56.71% and 22.11% of Cd^{2+}, respectively. In pot soil containing 50 and 100 $mg \cdot kg^{-1}$ of Cd^{2+}, strain KG2 caused a 45.9% and 35.3% decrease in soybean root Cd content, respectively. The strain KG2 improved the root and shoot length, nitrogen content and biomass of soybean plants and superoxide dismutase activity.

Recent strategies to increase biological nitrogen fixation (BNF) in legumes

Legumes have been approximately contributing 20% of the nitrogen required for overall grain and oilseed making. Owing to their advantageous assets, legumes potentially fix nearly 80% of their own N requirement, besides aiding as a supplement to the succeeding crops. However, all these potential benefits can be utilized merely in the assured situation. Pure legumes addition in a cropping practice does not guarantee high BNF. For exploitation of BNF, there lie two most common approaches, viz., first, enhanced crop, soil and water management to attain the utmost ability of BNF and second, inoculation of *Rhizobium* or selection of host genotypes to assure an elevated amount of nitrogen fixation in the plant. The rhizobia–legume symbiosis accounts for a significant proportion of nitrogen available to the leguminous crop. The use of efficient rhizobial strains as biofertilizers to enhance legume production is a significant method in sustainable agriculture (Saharan and Nehra 2011). Among both approaches, the first one is well recognized for approximately 50 years and will continue to play its correct function. While the second one on the host plant's choice is the latest. Therefore, there arises a requirement to enhance rhizobia for improving their symbiotic effectiveness and vast host choice. Recent advancements in the next-generation high-throughput techniques allows to explore the depth of biological nitrogen fixation. The omics-based techniques are highly efficient and informative for the enhancement of nitrogen fixation in the legumes (Afzal et al. 2020).

Plant growth-promoting rhizobacteria (PGPR) as multifunctional agents

Current agriculture faces challenges, for instance, impairment of soil productiveness, varying climatic parameters and increase in pathogen and pest attacks. Sustainability and environmental security of agricultural production rely on various eco-friendly tactics such as biofertilizers, biopesticides and crop residue management. The range of valuable microbial inoculants effects, mainly in plant growth promotion, indicates the need of further investigation for their exploitation in terms of present agriculture (Gopalakrishnan et al. 2015). PGPR promotes plant growth and development using several mechanisms such as the production of phytohormones, siderophore production, phosphate solubilisation and decrease of plant ethylene level by ACC utilization or nitrogen fixation associated with roots. Several bacterial isolates directly control plant physiology by mimicking the synthesis of phytohormones, whereas some enhance the availability of various minerals and nitrogen in the soil, thereby supplementing plant growth and development. Plants choose PGPR that is competitively well to inhabit niches without causing any pathological stress on them (Fig. 2). PGPR may use different mechanisms to augment the growth and development of the plant, as investigational proof suggests that the encouragement of plant growth is the net product of numerous tools that may be functioning at the same time. Sultana et al. (2019) isolated *Rhizobium* spp. that retained a symbiotic relationship with leguminous plants including *Sesbania bispinosa* by fixing N_2 through nodule formation. Several researches suggest that Exopolysaccharides (EPSs) are required for nodule formation. Rhizobial growth parameters as well as the EPS production are affected by the presence of pesticides. Table 3 provides a list of multifunctional microbial strains recovered from different species of *Sesbania*.

Phosphate solubilization

Among all macronutrients, phosphorus (P) is essential for plant growth and advancement aiding in photosynthesis, production of energy and sugar, besides improving nitrogen fixation in legumes. Only 0.1% of the P is accessible to plants from the total P content of soils, while the rest in an insoluble form, making it unavailable for plants uptake. Rock phosphate (RP) is the sole economic basis of P. However, its accessibility is limited and skewed. Generally, it is found to be in precipitated form (mono- or orthophosphate) in the soil or is adsorbed by Al or Fe oxides via ligand exchange. Mobilization of inaccessible P to plant-available P is must to prolong crop yields (Bhatt and Maheshwari 2020). Phosphate-solubilizing microorganisms (PSM) play a very significant function in transforming unavailable form of phosphorus to the available form, by lowering the soil pH, as a result producing organic acids, besides mineralization of organic phosphorus by acid phosphatases and alkaline phosphatases, thus making it available for plants uptake (Baby et al. 2016; Bhatt and Maheshwari 2019). Bacteria-solubilizing phosphate, i.e. PSB and PGPR altogether could decline the practice of phosphorus fertilizer by 50% without causing any adverse effect on the crop yield. The most significant PSB belonging to the genera, viz., *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas* and *Serratia*, are reported well. The ability of P-solubilization is found even among *Rhizobiacae*, comprising of *Rhizobium*, *Bradyrhizobium*, *Mesorhizobium* and other non-specified legume-nodulating bacteria (LNB). Singh and Gera (2018) reported that out of 20 *Sesbania grandiflora* rhizobia, around 80% of the isolates were able to form significant phosphate

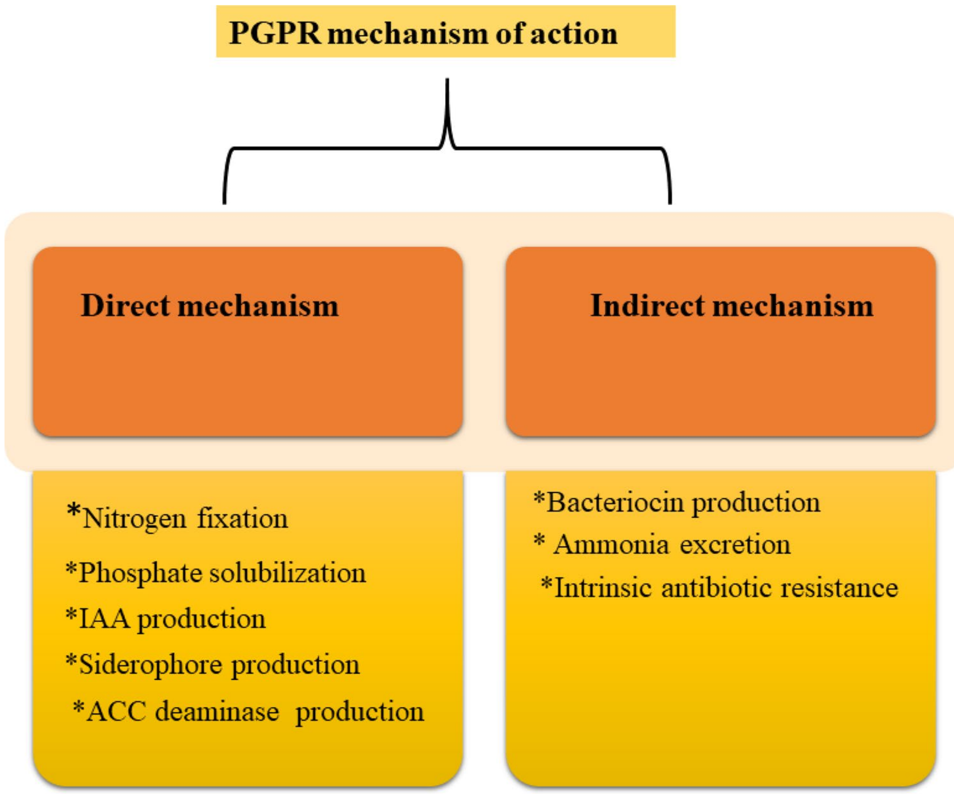

Fig. 2 Direct and indirect mechanisms of plant growth-promoting rhizobacteria (PGPR)

Table 2 *Sesbania* plants application as biofertilizer with various crops

Treatment	Crop	References
Sesbania rostrata	Growth and yield enhancement in rice	Latt et al. (2009); Naher et al. (2020)
Sesbania sesban in combination with urea and calcium carbide	Rice and wheat yield enhancement	Patra et al. (2006)
Sesbania sesban	Maize growth and yield	Phiri et al. (2003)
Sesbania aculeata and mungbean residues	Enhanced growth and yield in rice and wheat	Sharma et al. (1995)
Sesbania sesban	Yield enhancement in Maize	Kwesiga and Coe (1994)
Sesbania sesban	Improved fallows have potential to supply nutrients to maize and eliminate the need for P fertilizers on P-deficient soils	Jama et al. (1998)
Sesbania sesban	Yield enhancement and suppression of Striga infestation in maize crop	Matata et al. (2011)
Sesbania aculeata	Significantly increased soil biochemical properties and grain yield of rice–wheat system	Saikia et al. (2019)
Sesbania rostrata and *S. aculeata*	Improved rice yield and soil fertility	Ventura and Watanabe (1993)
Sesbania speciosa	Increased soil fertility and higher grain yield of rice	Weerakoon et al. (1992)
Sesbania aculeata	Improved productivity under flood-prone lowland conditions	Sharma and Ghosh (2000)
Sesbania aculeate and nitrogen fertilizers application	Higher grain yield of rice and improved soil properties	Islam et al. (2019)
Sesbania herbacea	Efficiently fix N_2 in flooded conditions	Krishnan et al. (2019)

Table 3 Multifunctional bacterial isolates associated with *Sesbania* plants

Sesbania spp.	Plant growth promotory rhizobacteria	Mechanism of enhanced plant growth	References
Sesbania bispinosa	*Pseudomonas fluorescens* DACG3, *Burkholderia* sp. DACG1	Enhanced biomass, root and shoot growth in Chickpea	Dasgupta et al. (2015)
Sesbania herbacea	*Rhizobium huautlense*	Nodulation and of the host plant under flooded as well as non-flooded conditions	Wang and Martinez-Romero (2000)
Sesbania cannabina	*Rhizobium* sp. U9709-SC	Phosphate solubilization	Daimon et al. (2006)
Sesbania cannabina	*Agrobacterium salinitolerance*	Promote salt endurance in the host plant	Yan et al. (2017)
Sesbania rostrata	*Sinorhizobium saheli*, *Ensifer*sp. AC01b	Bioremediation of glyphosate and monocrotophos	Chauhan et al. (2017)
Sesbania procumbens	*Rhizobium* sp.	Indole acetic acid production	Sridevi and Mallaiah, (2007a, b)
Sesbania sesban (L)	*Rhizobium* spp. (strain NEPMR1, NETBR1, NEANR1, NEPR1, NEAMBR1, NEBR1, NEKR1, NETR1)	Salinity and temperature tolerance	Nohwar et al. (2019)
Sesbania procumbens	*Rhizobium SBS-R1OO*	Improve soil fertility and ecological sustainability	Shenbagarathai and Shanmugasundaram (1993)
Sesbania punicea and *S. virgata*	*Azorhizobium doebereinerae*, *Rhizobium etli*	Increased dry matter production	Blanco et al. (2008)
Sesbania bispinosa, *S. cannabina*, *S. exasperata*, *S. formosa*, *S. grandiflora*, *S. madagascariensis*, *S. macrantha* and *S. pachycarpa*	*Rhizobium strain IRBG74*	Facilitate effective nodulation	Cummings et al. (2009)
Sesbania rostrata	*Methylobacterium* sp. strain NPFM-SB3	Produced indole-3-acetic acid, cytokinins and on inoculation to rice plants resulted in numerous lateral roots	Senthilkumar et al. (2009)
Sesbania rostrata	*Azorhizobium caulinodans* ORS571	Fix atmospheric nitrogen in free-living and symbiotic states	Liu et al. (2019)
Sesbania sesban	*Bacillus xiamenensis* PM14	Inoculated plants have positive effects on growth and metals accumulation by *S. sesban*	Din et al. (2020)
Sesbania sesban, *S. rostrata*	*Azorhizobia caulinodans*	Produced higher biomass than the uninoculated controls	Chan et al. (2003)

solubilization zone on the media supplemented with P (Pikovskaya's medium), where their solubilization index (SI) varied from 1.96 to 4.85.

Production of indole-3-acetic acid (IAA)

IAA is a growth phytohormone considered to be the most important representative of auxin class of plant hormone. Some common precursors for natural biosynthetic pathways are tryptophan and derivatives of indole. Microbes isolated from the rhizospheric region of different crops have the capability of IAA production, as secondary metabolites due to the rich supply of substrates. IAA functions as a regulator of several biological processes, viz., cell division, elongation and differentiation to tropic responses, seed germination, growth of root hairs, fruit development and senescence, thus performing a key role in plant growth and development. Parallel to plant, IAA also affects the survivability of bacteria along with its resistance to plant defence. As per the reported data, about 80% of rhizospheric microbes possess the capability of synthesizing and liberating auxins as secondary metabolites. Sridevi and Mallaiah (2007a, b) reported 26 IAA-producing *Rhizobium* strains from root nodules of *Sesbania sesban* (L.) Merr., from different locations of Andhra Pradesh. However, only five strains were able to produce the maximum amount of IAA in yeast extract mannitol (YEM) medium supplemented with L-tryptophan. Etesami et al. (2014) reported enhanced shoot biomass and root length after inoculation of seedlings (host plant) with IAA-producing isolates. IAA-producing bacteria enhanced the plant vegetative growth.

Siderophore production

Since iron is one of the requisite microelements for all living cells but its availability is limited, as the dominant form of iron in the soil is present as ferric iron (Fe^{3+}), which has very low solubility. Rhizospheric bacteria fix the atmospheric nitrogen in a symbiotic association with the leguminous plants via iron-containing enzyme nitrogenase. During evolution, microorganisms have established the strategies of acquiring and assimilating iron, by secreting iron chelators called siderophores. Siderophores chelate iron and alter it to a soluble form, and they are commonly produced by aerobic, facultatively anaerobic bacteria and fungi under iron-limiting conditions. Sridevi and Mallaiah 2008 studied 26 rhizobium strains isolated from root nodules of *Sesbania sesban* (L.) Merr. which were studied for their ability to produce siderophores. It was found that only nine strains have the ability to produce catechol-type of siderophores in culture after 4 h of incubation and at neutral pH. Mannitol and sucrose at the concentration 2% stimulated growth and siderophore production. To date, nearly 500 siderophores are reported from selected microorganisms. In general, siderophores are classified as hydroxamates, catecholate, salicylates, carboxylates and new group polycarboxylates (Kannahi and Senbagam 2014). Joshi et al. (2018) isolated siderophore-producing bacteria from agricultural soil belonging to genus *Pseudomonas* and maximum siderophore production was observed at 6.5 pH and 30 °C using glucose as the carbon source. The type of siderophore was determined and was found to be a hydroxamate type. Singh et al. (2018) reported that out of 14 *Sesbania sesban* rhizobia, 6 of them possess the capability of siderophore production on Chrome-Azurol S agar medium after 7 days of incubation.

1-Aminocyclopropane-1-carboxylate (ACC) deaminase activity

Symbiotic associations of rhizobia and legume are extremely significant with respect to sustainable agricultural practices. In regard to this, ethylene (phytohormone) plays a vital role in the process of nodule formation, where it acts as an inhibitor of the nodulation process (Lindstrom and Mousavi 2020). Among all the phytohormone, ethylene tends to be an important one, but its overproduction under stressful conditions directly affects the plant growth or death, especially for seedlings (Deng et al. 2020). Apart from this, ethylene may also be involved in various phases of symbiosis, including the initial response to bacterial nod factors, nodule development, senescence and abscission. To counter this, various bacteria possess the capability of production of an enzyme called ACC deaminase, which can decrease the levels of ethylene (Nadeem et al. 2020). The ACC deaminase works by the action of degradation of ACC (1-aminocyclopropane-1-carboxylate) to ammonia and α-ketobutyrate, followed by their metabolization both by bacteria and plant (Shahid et al. 2020). Besides, possessing a significant role in the nodulation process, ACC deaminase also modulates the persistence of nodules (Nascimento et al. 2016). Rhizobia, that expresses ACC deaminase enzyme, possess increased symbiotic potential. Plant growth-promoting bacteria (PGPB) producing ACC deaminase offers drought tolerance by regulating plant ethylene levels. Thus, PGPB that express ACC deaminase activity tends to protect plants growth from various unfavourable conditions, viz., flooding, drought, anoxia, high salt, fungal and bacterial pathogens, nematodes, metals and organic contaminants. The study of Chandra et al. (2019a, b); Chandra et al. (2020) and Saleem et al. (2018) reported inoculation of PGPR containing ACC deaminase enzyme in wheat, finger millet and *Velvet bean* could improve plant growth as compared to uninoculated plants under drought conditions.

Bacteriocin production

Bacteriocins are low-molecular-weight peptides or proteins which are extracellularly released by bacteria with the bactericidal or bacteriostatic mode of action, principally against a wide range of most closely related Gram-positive bacteria, but the producer cells are immune to their own bacteriocins (Baindara et al. 2018). Bacteriocins are well recognized to be produced by a number of Gram-positive and Gram-negative bacteria but Gram-negative bacteria are well studied for their bacteriocin production. The clear halo zone that resulted from the bacteriocin production by a particular strain in a grid was observed from the growth of the overlaid test strain (Kaskoniene et al. 2017). Strong bacteriocin production was observed by clear halo zones, while hazy zones interspersed with small, punctiform growth of the overlaid strain indicated weak bacteriocin production. Bacteriocin appears to play an important role in determining competitiveness for nodulation when assayed against some strains. Ansari and Rao (2014) assessed bacteriocin production in indigenous soybean rhizobia in vertosols of central India and other soils. The slow-growing soybean strain R33 strongly inhibited the growth of 19 rhizobia strains.

Ammonia excretion and intrinsic antibiotic resistance (IAR)

Ammonia production by rhizobia plays an important role in biocontrol activity, which may indirectly influence plant growth. *Rhizobium* spp. fixes atmospheric N_2 in symbiotic association with a leguminous plant. The main procedure, converting atmospheric nitrogen (N_2) to ammonia (NH_3) takes place inside the nodule symbiosome by the bacteroides via the nitrogenase enzyme complex, which tends to be oxygen sensitive which irreversibly damaged by oxygen. The ammonia formed in the bacteroides, however, is assimilated by plant enzymes in the plant cytosol. Several processes exist utilizing which ammonia can be produced, viz., nitrite ammonification, degradation and decarboxylation of amino acids to create biogenic amines with ammonia, deamination and the urease mediated hydrolytic degradation of urea. This form of ammonia cannot be utilized by plants but may be available through the BNF process, developed only in prokaryotic cells. Inoculation with such bacteria enhances plant growth as a result of their ability to convert atmospheric nitrogen (N_2) to ammonia (NH_3) making it an available nutrient for plant growth. Ammonia production was reported by Joseph et al. (2007) in 95% of total isolates of *Bacillus* followed by *Pseudomonas* (94.2%), *Rhizobium* (74.2%) and *Azotobacter* (45.0%).

The resistance of rhizobia refers to their intrinsic resistance to antibiotics in terms of usual development. The mode of action of antibiotics against any bacteria relies on the chemical constitutes of antibiotics, bacterial cell morphology and primary cell walls. The resistance of PGPR to several antibiotics might have an ecological advantage of survival in the rhizosphere when they are introduced as inoculums. Diverse rhizobial strains show distinct degrees of susceptibility to antibiotics, that is why this property is being meant for their identification. Antibiotics resistance of rhizobial strains (mutants) is extensively used in investigating their survivability in various environments including soil and for monitoring their competitiveness as a marker for nodulation of the host plant and effectiveness of nitrogen fixation. Different *Rhizobium* strains of faba bean and soybean were found to be resistant to different antibiotics, viz., amoxicillin, ampicillin and cloxacillin while very few strains were found to be resistant to ampicillin and cloxacillin only (Abera et al. 2015). Dhull et al. (2018) reported that out of most of the rhizobial strains had good growth on ampicillin, chloramphenicol, nalidixic acid and streptomycin up to concentrations of 100 $\mu g\ ml^{-1}$ while using gentamicin showed medium growth up to concentrations of 20 $\mu g\ ml^{-1}$. None of the rhizobial strains showed growth on the YEMA medium supplemented with antibiotics, viz., kanamycin, neomycin and tetracycline even at concentration of 10 $\mu g\ ml^{-1}$. The rhizobial strain GB-5c showed growth on all the antibiotics tested except kanamycin and neomycin. The potential indigenous microbial strains can be used for the large scale crop production which could reduce the harmful effects of chemical fertilizers (Fig. 3).

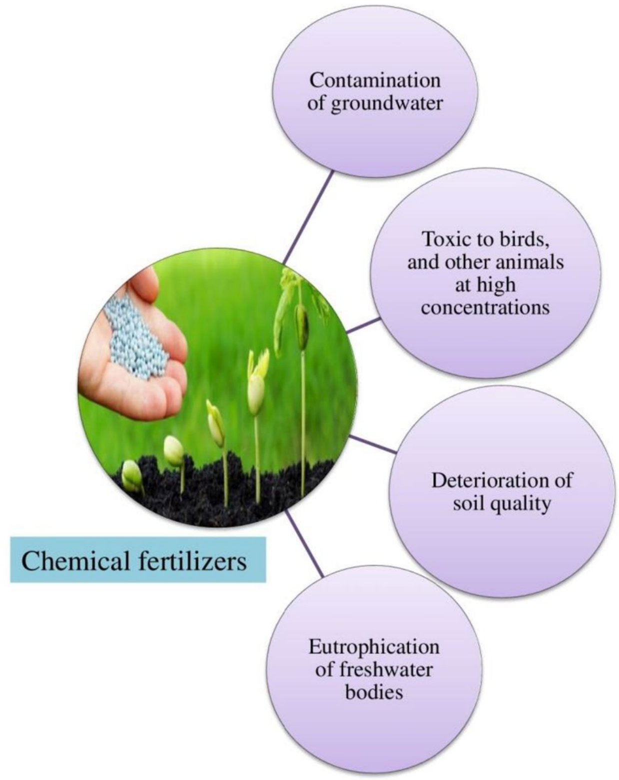

Fig. 3 Harmful effects of chemical fertilizers

Conclusions and future prospects

This study recognizes importance of *Sesbania* plants and their respective rhizobia as a non-polluting and more commercial way for improving soil fertility compared to other ways, such as application of chemical fertilizers, pesticides and sewage sludge. The fertility of the soil is of significant concern due to various alarming risks on human health because of the leaching of toxins from fertilizers and pesticides into the groundwater. *Sesbania* has multifarious attributes, making them attractive as multipurpose plants and potentially useful species in agricultural production systems. *Sesbania* rhizobia is superior to other N_2-fixing systems with high N_2-fixing potential. *Sesbania* plants and their rhizobia are useful because they have the capability of adapting to acidic, alkaline and waterlogging soil conditions. Various symbionts including seven novel genospecies within *Agrobacterium*, *Ensifer*, *Neorhizobium* and *Rhizobium* were identified among the *S. cannabina* rhizobia and all of them were designated as symbiovar *sesbaniae* based on their highly conserved symbiosis genes and nodulation test results. To achieve the maximum legume productivity, screening of native isolates for high-nitrogen fixation efficiencies tends to be significant. Several *Sesbania* plant rhizobia capable of tolerating extreme conditions of alkalinity, acidity, salinity, drought, metal toxicity and fertilizer were identified. In fact, the existence of *Rhizobium*-tree legume symbiosis, capable of fixing the appreciable amount of N_2 under severe conditions, is fascinating. Thus, *Sesbania* represents the best source of ideal fertilizers in the present and subsequent crops, and therefore, commands great interest as the subject of future research. There is a need to implement the use of *Sesbania* plants and their respective rhizobia as biofertilizer from lab to field so that in the upcoming years, soil health is maintained and the problem of soil infertility can be diminished. Recent high-throughput tools and techniques in the future can also help to increase our understanding of the *Sesbania* plants and their associated microbes.

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Compliance with ethical standards

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

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