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REVIEW ARTICLE

Rhizobium as Biotechnological Tools for Green Solutions: An Environment-Friendly Approach for Sustainable Crop Production in the Modern Era of Climate Change

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Abstract

Modern and industrialized agriculture enhanced farm output during the last few decades, but it became possible at the cost of agricultural sustainability. Industrialized agriculture focussed only on the increase in crop productivity and the technologies involved were supply-driven, where enough synthetic chemicals were applied and natural resources were overexploited with the erosion of genetic diversity and biodiversity. Nitrogen is an essential nutrient required for plant growth and development. Even though nitrogen is available in large quantities in the atmosphere, it cannot be utilized by plants directly with the only exception of legumes which have the unique ability to fix atmospheric nitrogen and the process is known as biological nitrogen fixation (BNF). *Rhizobium*, a group of gram-negative soil bacteria, helps in the formation of root nodules in legumes and takes part in the BNF. The BNF has great significance in agriculture as it acts as a fertility restorer in soil. Continuous cereal–cereal cropping system, which is predominant in a major part of the world, often results in a decline in soil fertility, while legumes add nitrogen and improve the availability of other nutrients too. In the present context of the declining trend of the yield of some important crops and cropping systems, it is the need of the hour for enriching soil health to achieve agricultural sustainability, where *Rhizobium* can play a magnificent role. Though the role of *Rhizobium* in biological nitrogen fixation is well documented, their behaviour and performance in different agricultural environments need to be studied further for a better understanding. In the article, an attempt has been made to give an insight into the behaviour, performance and mode of action of different *Rhizobium* species and strains under versatile conditions.

Introduction

The world population will be 9.7 billion by 2050 and 11 billion by 2100 and agriculture will play a crucial role to feed a huge population with deteriorating and shrinking natural resources [1]. World agriculture experienced a quantum growth in farm output during the second half of the previous century and simultaneously witnessed a decline and shrinkage of natural resources. In the last quarter of the twentieth century, yield plateauing of important crops and cropping systems was also observed worldwide [2]. The supply-driven technologies of modern agriculture relied mostly on the application of huge synthetic chemical inputs and few high-yielding varieties and hybrids of crops. Also, it ignored the optimum use of natural resources, maintenance of crop diversity and biodiversity and creation of a healthy agroecosystem. All these practices ultimately caused havoc on agricultural sustainability. To meet the food demand of the rising population, agriculture needs to be more productive, resilient and resource-efficient under the present consequences of limited resources and climate change issues [2]. However, excessive and injudicious application of fertilizers may negatively affect the environment [3]. Injudicious application of fertilizers has resulted in many ill effects such as groundwater pollution, increased greenhouse gas emission, poor soil health and so on. Unless resources are judiciously used and soil health is taken care of, it will be difficult to maintain the long-term productivity of soils. Considering the ill effects of excessive use of chemical fertilizers, alternate

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nutrient sources such as biofertilizers, organic manures, composts, etc., need to be promoted for ensuring a sustainable production system.

Soil health improvement and management are important aspects of achieving agricultural sustainability. Soil health is a complex as well as a dynamic feature, where physical, chemical and biological properties collectively interact. As soil is a tremendous biological laboratory, microorganisms play a significant role in maintaining soil health. Research carried out in physiological, biochemical and molecular studies on the relationship between plants and microbes clearly indicated the role of microbes in soil biota [4]. Several beneficial soil microorganisms promote plant growth, fix atmospheric nitrogen, mineralize, solubilize and mobilize unavailable plant nutrients [5, 6], and mitigate various biotic and abiotic stresses [7, 8]. The microbial strains that fix atmospheric nitrogen, and mobilize and solubilize different unavailable forms of soil nutrients are known as biofertilizers. Biofertilizers have been found to improve crop growth and productivity through different activities such as nitrogen fixation, nutrient solubilization, the release of growth-promoting substances or disease suppressiveness activity [9]. Moreover, unlike chemical fertilizers, they do not have any negative impacts on the environment. The dependence on chemical fertilizers can also be reduced to some extent by the use of biofertilizers. Considering these benefits, the use of biofertilizers is promoted in different crop production systems. Rhizobium is one such organism which fixes atmospheric nitrogen through the biological nitrogen fixation process and improves soil fertility [10]. Nitrogen is an essential plant nutrient and helps in the growth and development of plants [11]. Most agricultural soils are deficient in nitrogen. Poor soil organic matter status, soil erosion, continuous cultivation of cereals, etc., may reduce the soil nitrogen status [12]. Nitrogen is a highly mobile nutrient and is subjected to various loss mechanisms such as leaching, denitrification, ammonia volatilization, etc., which further reduces soil nitrogen content. Unless this nitrogen loss from the soil is replenished, it will be difficult to maintain the yield level. Even though the atmosphere contains a high amount of nitrogen, it cannot be directly utilized by most crop plants [13]. However, the legumes have the unique ability to fix atmospheric nitrogen. Rhizobium in a symbiotic relationship with legumes can fix atmospheric nitrogen and improve soil fertility as well as soil health [14].

In the modern era of climate change, anthropogenic intervention in agriculture in the form of fossil fuel burning contributes a lot to the production of greenhouse gases causing global warming. The contribution of greenhouse gases (GHGs) from agriculture was 11% of human GHGs emissions [15]. In arable lands, to supply nitrogen to crops, different synthetic chemical fertilizers are applied. Urea is the most commonly and widely used nitrogenous fertilizer that releases GHGs such as methane, nitrous oxide and carbon dioxide from the crop field. On a global scale, the annual production of nitrogenous fertilizer causes the emission of approximately 300 Tg of CO_2-equivalent GHGs into the atmosphere [16]. To overcome the threat of global warming as well as climate change in agriculture, there is an urgent need for the adoption of mitigation and adaptation options. The above contexts suggest the use of alternative sources of nutrient application targeting the evergreen revolution as well as agricultural sustainability. In this direction, biofertilizers can play a pivotal role.

There is no doubt that the use of chemical nitrogen fertilizers has greatly increased in the last few decades. Nitrogenous fertilizer is effective in improving crop yield; however, they are also subjected to different losses such as leaching [17], denitrification [18] and ammonia volatilization [19]. However, the biologically fixed nitrogen is less susceptible to these losses [20]. In addition to nitrogen fixation, Rhizobium can also protect the host plant against pathogens and diseases. The possible mechanisms for disease and pest resistance include competition for nutrients, antibiosis or induced resistance in the host plant [20]. The overall growth improvement brought about by Rhizobium can be attributed to biological nitrogen fixation, improved phosphorus solubilization [21], siderophore production [22] and phytohormone production [23]. Considering the benefits of Rhizobium (Fig. 1), it can be used as a biofertilizer for improving soil fertility and crop productivity, especially for legumes and legume-based cropping systems. Moreover, the nitrogen fixed by *Rhizobium* may be available to the subsequent crop.

Rhizobium: Discovery and Classification

Rhizobium comes from two Greek words 'rhiza' means a root and 'bios' means life. Beijerinck [24] isolated the bacterium from the root nodules and called it as "*Bacillus radicicola*". Further Frank [25] named it as "*Rhizobium leguminosarum*". The symbiotic bacteria belonging to the genera *Rhizobium* can be collectively called as "rhizobia". This group of bacteria belong to the classes of alpha- and beta-proteobacteria. Rhizobia can be broadly divided into two classes based on the characteristics of its development. Fast-growing Rhizobia produce acid on yeast mannitol medium and it includes *R. trifolii*, *R. phaseoli*, *R. Meliloti, R. leguminosarum* and the others. Slow-growing strains produce alkali on yeast mannitol medium and it includes *Bradyrhizobium japonicum* [26], Sinorhizobium [27] and Mesorhizobium [28]. Rhizobia strains are gram-negative, non-spore-forming, motile, aerobic rods and heterotrophic. Generally, fast-growing rhizobia grow vigorously with most sources of carbohydrates while the slow growers are more specific in their requirements, and can utilize sodium citrate,

Fig. 1 Beneficial roles of *Rhizobium* for crop production

xylose, mannitol, arabinose, galactose, fructose and rarely dextran [29]. Different Rhizobia strains and their host specificity are listed in Table 1.

Biological Nitrogen Fixation

Mechanisms of Biological Nitrogen Fixation

The conversion of atmospheric nitrogen to ammonia (NH_3) is known as nitrogen fixation. The nitrogen-fixing bacteria, whether free-living or symbiotic, trap atmospheric nitrogen and convert it to NH_3 for utilization by plants, a process known as biological nitrogen fixation (BNF). This reaction is catalysed by the oxygen-sensitive enzyme nitrogenase, which is found within the bacteria. The process can be summarized in the following reaction:

$$N_2 + 8H + 8e^- + 16ATP \xrightarrow{\text{Nitrogenase}} 2NH_3 + H_2 + 16ADP + 16Pi$$

Biological nitrogen fixation is catalysed by the enzyme nitrogenase, which is found in microorganisms from practically every taxonomic class. Nitrogenase catalyses the reduction of nitrogen gas to ammonia. Nitrogenase is made up of two oxygen-labile metalloproteins i.e. dinitrogenase and dinitrogenase reductase. Dinitrogenase is a 240-KDa tetramer of the nifD and nifK gene products alpha2-2. Dinitrogenase reductase is a 60-kDa alpha2 dimer with a single 4Fe-4S centre that is coordinated between the two nifH gene products' subunits [30]. The connection of several gene clusters completes the nitrogen-fixing process [31]. It is crucial to understand how fixed nitrogen affects the supply of nitrogenase to develop techniques for increasing the quantity of ammonia produced by nitrogen-fixing bacteria that may be employed in agriculture [32]. During catalysis, electrons are transferred one at a time to the MoFe protein, in a process that involves component–protein contact, dissociation and hydrolysis of at least two MgATPs for each electron transfer. The MgATP binding and hydrolysis sites are found in the Fe protein, while the substrate binding and

Table 1 Cross-inoculation groups of Rhizobium

Genus	Species	Crops
Rhizobium sp.	*R.meliloti*	Alfaalfa, Sweet clover
	R.leguminosaraum bv. Vicieae	Pea, Lentil, Lathyrus
	R.leguminosaraum bv. Phaseoli	Beans
	R.leguminosaraum bv. Trifolli	Clover
	R.fredii or S.fredii,	Soybean, Pigeonpea
	R.lupin	Mung, Urd bean
	R.phaseoli	Gram
	R.trifolii	Alfalfa
Bradyrhizobium sp.	*B. japonicum, B. elkanii*	Soybean
	B. liaoningense *Bradyrhizobium* species	Cowpea, Mungbean, Chickpea, Pigeon pea, Chickpea, Groundnut, Sun hemp
Mesorhizobium sp.	*M. loti*	Birds foot trefoil
	M. huakuii *M. mediterraneum*	Cicer, milkvetch
	M. cicero	Chickpea
Sinorhizobium sp.	*S. meliloti*	Alfalfa
	S. meliloti	Sweet clover
	S. medicae	Annual medics

reduction sites are found in the MoFe protein. Aside from the traditional Mo-containing nitrogenase, *Azotobacter vinelandii* has been found to have two different nitrogenases, one with vanadium (V) as a co-factor and the other with only iron (Fe) as a co-factor. V-nitrogenase has also been found in *A. chroococcum* and *Anabaena variabilis* [33]. The regulatory genes *nif* L and *nif* A are found on the chromosomes of *Azotobacter vinelandii*. *Nif* A binds to the promoters of all operons, allowing the *nif* genes to be produced [34].

Mechanism of Symbiosis Specificity and Rhizobium–Legume Interaction

A wide range of host and bacterial genes are involved in various modes of action which regulate diverse symbiotic specificity [35]. The compatibility of two symbiotic partners with each other is essential for a successful symbiosis. In case of incompatibility, the bacteria cannot form nodules and subsequent nitrogen fixation. Many pathogenic bacteria produce similar signalling molecules to symbiotic bacteria. But the host has a separate recognition mechanism to distinguish between pathogenic and symbiotic bacteria [36]. In legumes, the immune system distinguishes between the pathogenic and symbiotic bacteria with the help of receptors [37]. The genetic features of the host plant have a pronounced impact on the effects of symbiosis [38].

Factors Affecting the Activity of Rhizobium

Rhizobium activity in soil is affected by many factors such as temperature, soil moisture, soil organic matter, soil reaction and soil fertility [39] (Fig. 2). All the factors have been briefly discussed below:

Temperature

Temperature is one of the key environmental factors that influence various microbial processes and populations in the soil [40]. The rhizobial strain tolerance to elevated temperature in soil determines the extent of nodulation in the succeeding crop in tropical regions. Montanez et al. [41] reported that the optimum temperature that favours the growth of rhizobium was 25 °C and the nitrogen fixation ability of *Bradyrhizobium* declines both with higher and lower temperatures viz., 15 °C and 35 °C, respectively. The nitrogen-fixing ability of a rhizobial strain is highly sensitive to root temperature in legumes [42]. However, the critical root temperature at which enhanced activity of root nodules was observed varies from one strain to another [43]. Based on the optimum temperature requirement the rhizobial strains were classified into three types, viz., psychrophiles, mesophiles and thermophiles. Phychrophiles include those stains that prefer low temperatures (<10 °C) for their growth and development, mesophiles include those strains of rhizobium which prefer a temperature range of 20 to 45 °C as ideal for its growth and lastly, thermophiles include those

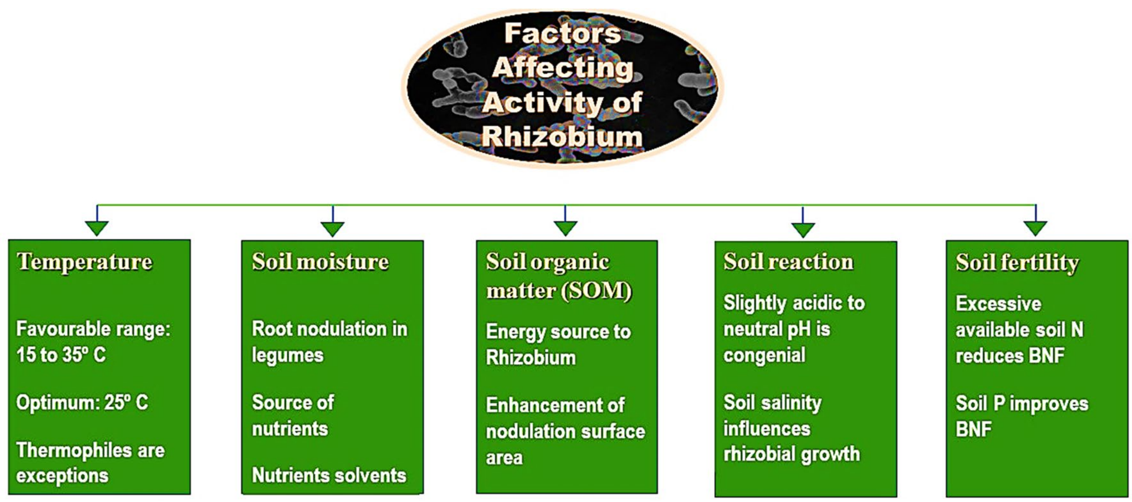

Fig. 2 Factors affecting the activities of *Rhizobium*

strains which prefer 45 to 60 °C as ideal for its activity under optimum moisture condition [44]. The temperature above and below the optimum range adversely affects the *Rhizobium* activity. The microbial process and population in the soil fall to a minimum when *Rhizobium* is exposed to low temperatures below its optimum and resumes back to normal with the increase in temperature.

Soil Moisture

Soil moisture is one of the key factors that determine the rhizobial activity in the soil. Soil moisture has a two-fold influence on rhizobium activity. Firstly, it acts as a source of nutrients to the bacteria and secondly, it acts as a solvent or carrier that improves the supply of nutrients to bacteria [45]. Inadequate soil moisture was reported to cause adverse effects on the survival, growth and population of *Rhizobium* in the soil. Consequently, affecting plant root nodulation, leghaemoglobin synthesis and nitrogen fixation. Recently, it was observed that under a limited supply of water, the plant nitrogen acquisition from nodules was minimized and the accumulation of products of fixation in the root nodule limited the nitrogen-fixing capacity of *Rhizobium* [46]. Similarly, in a study, it was indicated that nitrification and nitrogen cycling was influenced by soil moisture due to significant inhibition of the soil enzymatic system [47].

Soil Organic Matter

Soil organic matter is the chief source of energy for all soil microorganisms. There is both direct and indirect influence of soil organic matter on rhizobial activity. The residual *Rhizobium* population in the soil was determined by the organic matter content in the soil [39]. On the other hand, the influence of organic matter on soil properties facilitates the exploration of roots to deeper layers increasing the nodulating area and resulting in increased nitrogen fixation [12].

Soil Reaction

The soil reaction is another condition that significantly influences soil biological properties. Optimum pH is correlated with increased availability of water and nutrients attributing to the growth of plants as well as microorganisms [48]. As rhizobium is symbiotic nitrogen-fixing bacteria, while the ideal root growth also facilitates enhanced nitrogen fixation. A slightly acidic to neutral pH is ideal for the proper growth of *Rhizobium*. However, some strains of rhizobium were reported to perform well under a wider pH range offering a great potential to adapt to salinity stress [49]. *Rhizobium* strains were mainly classified into two types viz. fast-growing Rhizobium (*Rhizobium* strain) and slow-growing *Rhizobium* (*Bradyrhizobium* strain) [50]. Both fast and slow-growing strains of rhizobium vary in their adaptation to salinity, and studies reported that fast-growing *Rhizobium* species were more tolerant to high salinity than slow-growing rhizobium strains [51]. In a study, it was observed that when the root hair of soybean was inoculated with the slow-growing *Rhizobium japonicum,* the root hair curling was intensified with the increase in the salt concentration from 1 to 1.5% NaCl concentration and seriously limiting the nitrogen fixation [52].

Soil Fertility

Rhizobium is the most popular bacteria associated with symbiotic nitrogen fixation with legumes. The role of *Rhizobium* in fixing an adequate quantity of nitrogen established self-sufficiency in legumes to nitrogen [53]. However, residual soil fertility is playing pivotal importance in determining the response of *Rhizobium* in the soil. Recent studies indicated decreased response of *Rhizobium* with increased concentration of nitrogen [54]. Reinprecht et al. [55] realized that biological nitrogen fixation was inhibited with the increase in nitrogen supplementation from 30 to 100 kg/ha, respectively. In contrast, *Rhizobium* has a synergistic response with the soil's available phosphorus. Similarly, in a study, it was found that significant improvement in the concentration of soil-available phosphorus attributed to better rood growth and contributed to the formation of root nodules [56].

Rhizobium Inoculants Application as Biofertilizer

Among different biofertilizers, *Rhizobium* is a microbial bio-inoculant that is substantially more effective and commonly utilized. *Rhizobium* fixes atmospheric nitrogen in collaboration with legumes and the process is commonly known as biological nitrogen fixation (BNF). The production of root nodules by legumes and their symbiotic relationship with the *Rhizobium* bacterium results in the fixation of atmospheric nitrogen (Fig. 3).

The availability of a suitable stain for a certain legume is critical for successful rhizobium nodulation of leguminous crops. The presence of legume crops in the field affects the *Rhizobium* population in the soil. In the absence of legumes, the *Rhizobium* population in the soil decreases. Legumes get a significant proportion of their nitrogen requirement through BNF with effective *Rhizobia* in their root or stem nodules [57]. In nitrogen-deficient soils where other growth factors are at the optimal level, legumes have better survivability over their non-legume counterparts due to this symbiotic feature. Nodulation and nitrogen fixation are interactive processes that involve rhizobial nod factors. Some *Rhizobia* may produce phytohormones such as gibberellic acid, IAA and cytokinins that promote plant growth and development [58]. An improvement in seed germination, nodulation and plant growth in pea and vetch, as well as pod yield in pea, were found to be improved by nod factors isolated from *Rhizobium leguminosarum* [59]. In soybean and other non-leguminous crops, nod factors from *Bradyrhizobium japonicum* strain 532C increased germination and early plant growth.

Rhizobia have also been reported to improve rhizosphere nutrient availability, especially, that of nitrogen and phosphorus, producing pathogen-inhibiting compounds, and changing rhizosphere chemistry by regulating ethylene levels [60]. Several legumes, such as soybean, mung bean, chickpea, common bean, cowpea, Bambara groundnut and Kersting's groundnut have demonstrated the importance of the legume–rhizobia symbiosis in improving crop growth and productivity [61]. It is critical to choose a *Rhizobium* strain that is specifically suited to a given host plant. The only approach to achieve maximal nitrogen fixation and yields of leguminous crops is to carefully match Rhizobium strains with host plants and to employ largely viable inoculates made with this organism.

Rhizobium inoculation in legumes with appropriate strains results in higher growth and yield. *Rhizobium* strain EAL-1018 resulted in a 45.6% higher grain yield in faba bean over control [62]. Nyaga and Njeru [63] reported that native soil *Rhizobium* recorded higher growth and production of cowpea than commercial *Rhizobium* in sub-Saharan Africa [63]. The legume chickpea treated with P application along with *Rhizobium* seed inoculation increased root nodulation, growth and yield as compared to the application of

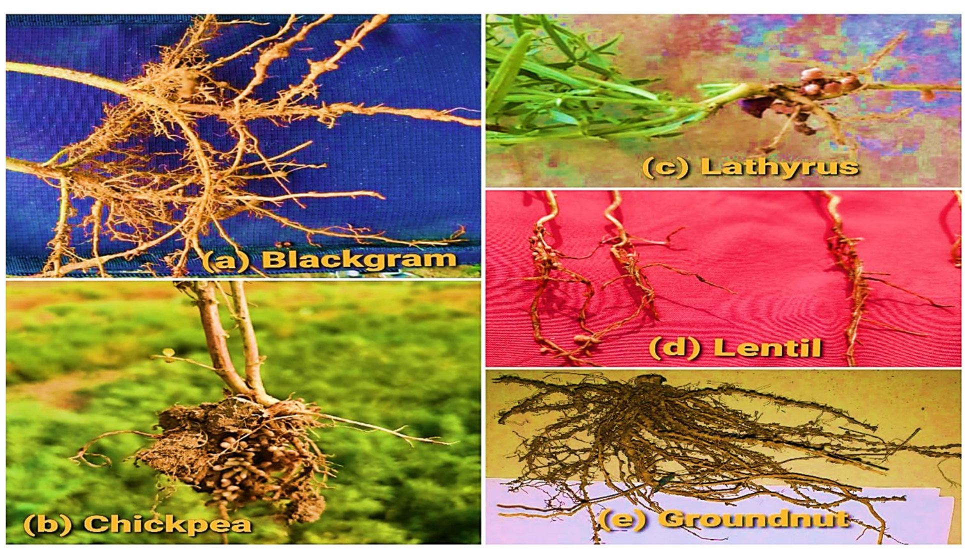

Fig. 3 Nodulation in different pulses, **a** blackgram, **b** chickpea, **c** *Lathyrus*, **d** lentil, **e** groundnut (Authors' own collected unpublished material)

P and *Rhizobium* alone [64]. An increase in no. of effective root nodules per plant, root and shoot dry weight of groundnut was observed due to rhizobial inoculation [65].

Many pieces of evidence are also available on the effect of *Rhizobium* on non-legumes. In wheat, maize and barley, inoculated with *R. leguminosarum* bv. *Trifolii* strain R39 showed a significantly 6–8% higher yield over uninoculated crops [66]. Seed inoculation and soil application of sunflower with *Rhizobium sp*. Strain YAS34 increased by 70 and 50% in root and shoot diameter, respectively [67]. Antoun et al. [68] proved that there was a beneficial effect of *Rhizobium* and *Bradyrhizobium* on radish dry matter production. Not only growth and yield parameters, cotton seed inoculation with *Rhizobium leguminosarum* bv *trifolii* (E11) also improved K^+ and Ca^{2+} ion uptake over uninoculated cotton [69].

Improvement in crop quality due to rhizobium application has also been reported. *Rhizobium* improved the protein content of peas [70]. Khaitov et al. [39] reported that the quality parameter such as protein and oil content along with grain yield of two chickpea genotypes Halima and Flip 06-66 showed higher values with inoculation of *Rhizobium* strains R6 and R9 on saline soil. The amount of nitrogen fixation by different grain legumes is shown in Table 2.

Application of Rhizobium-Based Biofertilizer in Crops Production

Seed Inoculation

Seed inoculation is common with pulses. In general, 250–375 g/ha of inoculant (solid carrier based) is required for seed inoculation in cowpea [75]. However, the amount of inoculant required varies depending on the size of the seeds. The inoculant is mixed with 200 ml of rice gruel to generate a slurry or any other starch solution of 2.5% concentration for the stickiness of the inoculant with the seeds needed to ensure a uniform coating [75]. After that, the seeds are dried in the shade for about 30 min. The treated seeds when dried can be sown immediately and preferably within 24 h the seeds should be sown. Among different *Rhizobium* inoculation methods, seed inoculation is a widely adopted and earlier several studies evidenced the significant yield enhancement in grain legumes (Table 3).

Table 2 Nitrogen fixation by different grain legumes

Grain legumes	Nitrogen fixation (kg/ha)	References
Chickpea	64–103	[71]
Lentil	35–100	[72]
Common bean	3–57	[72]
Cowpea	14–35	[73]
Pea	90–128	[74]

Seedling Inoculation

The seedling inoculation method is suitable for transplanted crops. In this method, 500 g of the inoculant is mixed in 40 L of water. The root portion of the seedlings required for an acre is dipped in the mixture for 5 to 10 min and then transplanted. However, Agba et al. [78] inoculated perennial crop *Mucuna flagellipes* seedlings by injecting 2 ml *Rhizobium* strains (16 colonies) in the yeast mannitol broth and recorded higher seed yield.

Soil Application

In the case of biofertilizer, generally, 750–1000 g of solid carrier-based inoculant is mixed with 20 kg of dried and powdered farmyard manure or the vermicompost and then broadcast in one acre of the main field just before transplanting. But, in legumes, seed pelleting inoculation of *Rhizobium* is a common practice and research evidence on soil application of rhizobium inoculant is meagre.

Rhizobium in Microbial Consortium and Co-culture

Considering the specific nutritional role of Rhizobium in nitrogen fixation, attempts are being made to develop consortia of microorganisms that cater to multiple nutritional needs of plant and other ecosystem services arising out from them. The microbial consortium has the distinct advantage of ease of application, lesser cost as compared to individual inoculations and multiplicity of use. In microbial consortia, two or more microorganisms are involved whose interaction is required to provide additive or synergistic results for better performance of a consortium [79]. The interactions in a consortium may vary depending on the microorganisms and/or the strains used in preparing the consortia. It can be said that for a successful consortium to be used for crop production purposes, consortia members should interact certainly. Positive interactions may

Table 3 Yield improvement in pulses due to rhizobium seed inoculation

Crops	Latin name	Yield increase (%)	Application methods	References
Lentil	*Lens culinaris* Medik	30–64%	Seed inoculation	[76]
Chickpea	*Cicer arietinum* L	19–36%	Seed inoculation	[39]
Soybean	*Glycine max* L	12–18%	Seed inoculation	[77]

arise out of cross-feeding where a bacterium utilizes the metabolic products produced by another microbe. Positive interactions can take the form of mutualism, protocooperation or commensalism.

Rhizobium is a common rhizosphere or soil inhabitant and hence, has direct competition and/or synergism with other microbes. The non-rhizobium bacteria (NRB) have been found to improve the activity of rhizobium in terms of nodulation and overall legume crop growth. Such beneficial interaction should be exploited to develop consortia or co-culture to derive maximum benefits out of the microbial application in crop production. NRB partners such as *Bacillus*, *Paenibacillus*, *Pseudomonas*, *Azospirillum*, etc., can be explored to be used in consortium or as a co-culture with rhizobium to get multiple benefits.

Role of *Rhizobium* in Improving Plant Stress Tolerance

In the present context of global warming and climate change, crops are facing tremendous pressure due to abiotic stresses. There are several adaptation options for crop management as a safeguard from the ill effects of abiotic stresses. Like other microorganisms, *Rhizobi*a have the potential to support crops under adverse climatic conditions and abiotic stresses. Rhizobia are well known to support legumes for biological N-fixation in a symbiotic association through the formation of nodules in roots. However, they play vital roles in the amelioration of abiotic stress in plants [80]. In general, in the process of alleviation of abiotic stresses, microorganisms induce some alterations in the physiological and metabolic activities of plants such as phytohormones activity, antioxidant defense, production of volatile organic compounds, trehalose, osmolytes, ACC deaminase, catalase, exopolysaccharides, chaperons and sugars [81] and enhances the availability of essential nutrients [82] by mechanisms such as phosphate solubilization. The role of *Rhizobium* in imparting stress tolerance in the crop has become a study of interest in the recent past. Many research works have been conducted on this aspect [83]. Selected isolates of rhizobium i.e. *Rhizobium leguminosarum* (LR-30), *Mesorhizobium ciceri* (CR-30 and CR-39), and *Rhizobium phaseoli* (MR-2) improved drought tolerance index in wheat seedlings, which have been attributed to the production of indole acetic acid by the selected isolates, which improved seedling root length [82].

Use of Suitable Rhizobium Strain Under Different Abiotic Stresses

Rhizobium inocula are often subjected to harsh soil environment. However, many strains of rhizobium have been found to perform under such conditions. Identification of such strains that can tolerate specific abiotic stress environments can be of great use in developing suitable bio-inoculation strategies at specific locations. A few pieces of evidence in this regard have been discussed below.

Two mutant drought-tolerant strains of *Rhizobium meliloti*, i.e. UL 136 and UL 222 outnumbered naturally present alfalfa *Rhizobia* and resulted in improved alfalfa growth, nodule growth and ultimately higher nitrogen fixation under water stress conditions [84]. Zahran and Sprent [85] reported that when drought-stressed *Vicia faba* plant was inoculated with *Rhizobium* species isolated from wild plants in the northern deserts of Egypt they produced effective nodules. Heat-tolerant strains of *Rhizobium*, e.g. *Rhizobium leguminosarum* pv. phaseoli formed effective symbiosis as well as nodule formation with the host bean plant even at high soil temperatures, i.e. 35 to 40 ℃, where most of the usual *Rhizobium* species become ineffective [86]. Survival and abundance of various *Rhizobium* species get affected by soil salinity but some salt-tolerant *Rhizobium* species help to overcome the adverse effect of soil salinity by specific morphological and metabolic changes and form effective symbiotic association with the host plants. Locally isolated strains of *Rhizobium meliloti* overcame the salinity stress successfully, and formed effective nodules on the host Medicago sativa plant even at a salinity level equivalent to 100 mM NaCl compared to other imported *Rhizobium* strains [87]. Individual Rhizobium strain, the combination of different *Rhizobia* species and strains and microbial consortia containing *Rhizobia* was known to support the plants under abiotic stresses. Not only in legumes, but Rhizobia play an important role in non-legumes such as wheat [81] and maize [82]. In non-legumes, Rhizobia form biofilms on abiotic and biotic surfaces letting nutrient dispersion and liquid flow. It may be a single species of Rhizobium or co-inoculation of different species of Rhizobia and other microorganisms, they support the plants in combatting abiotic stresses (Table 4).

Advancements in Rhizobium Technology

Many advancements have been recorded in *Rhizobium* technology in the recent past. Two significant developments in this direction have been discussed below:

Stress Response Genes for Improving Rhizobium Performance

Interventions to improve the performance of different strains in terms of improved nitrogen fixation, better crop growth promotion and tolerance to different stresses can be very useful. Successful host root colonization requires the *Rhizobium* to survive many adverse conditions in soil as well as host plant root. Stress response genes, such as otsAB, groEL,

Table 4 Rhizobia and co-inoculation of microorganisms in abiotic stresses alleviation

Crops	Rhizobia and other microorganisms	Abiotic stress	References
Legumes			
Chinese Milk Vetch (*Astragalus sinicus*)	*Mesorhizobium huakuii* strain 7653R	Drought	[88]
Groundnut (*Arachis hypogaea*)	*Rhizobium etli*	Salinity	[89]
Pea (*Pisum sativum*)	*Rhizobium* sp.	Ni, Zn toxicity	[90]
Green gram (*Vigna radiata*)	*Bradyrhizobium*	Ni, Zn toxicity	[91]
Lupine (*Lupinus luteus*)	*Bradyrhizobium*, *Pseudomonas* and *Ochrobactrum cytisi*	Cd, Cu and Pb toxicity	[92]
Non-legumes			
Wheat	*Rhizobium leguminosarum* and *Mesorhizobium ciceri*	Drought	[93]
Wheat	*Rhizobium leguminosarum*, strains y LCS2403, LBM1210, LET4910 and LPZ2704	Drought	[81]
Maize	*Rhizobium* and *Pseudomonas* sp.	Salinity	[94]

clpB and rpoH play a key role in providing stress tolerance to free-living *Rhizobia* [95]. Some of the stress response genes have been found to improve symbiotic effectiveness [95]. The microbial diversity under different adverse environmental conditions can be exploited to develop more efficient rhizobial inoculants. Overexpression of stress response genes in rhizobia to improve their symbiotic performance under adverse environmental conditions such as salinity, heat, drought stress and biotic stress have been reported by de Silva et al. [95]. This approach to improve rhizobium performance needs to be tested further with multiple strains and crops to evaluate their performance stability across different environments.

Advances in Rhizobial Inoculant Formulation

Successful commercialization of *Rhizobium* requires a formulation that is viable, cost effective and user friendly. The formulation should be prepared in such a way that it maintains the microbial cells in a metabolically and physiologically active state [96]. The presently available formulations include solid carrier-based formulations, liquid formulations, synthetic polymer-based formulations or metabolic-based formulations [97]. Each of the available techniques has some limitation which needs to be overcome to make a formulation technology that can be accepted globally. Many advanced formulations have been developed in this regard. The electrospinning technique of rhizobia immobilization has been tested [98]. Rhizobia inoculated into PVA nanofiber showed great promise in terms of the controlled release of bacteria and the formation of a large number of nodules [98].

Nanotechnology and Rhizobium Technology

Nanotechnology opens up a new frontier in biological nitrogen fixation research. The construction of an efficient symbiotic nitrogen fixation system using nanoparticles has been studied [99]. Induction of super conventional nodulation using manganese ferrite nanoparticles has been studied in soybean [99]. The nanobiotechnological approach for improving nodulation and crop performance can be effective by improving biological nitrogen fixation. Several studies indicate the detrimental effects of nanoparticles on rhizobial association, while there are also reports suggesting a stimulatory effect of nanoparticles [99]. The variation in impact might be due to the level of exposure, type of nanomaterials or stage at which the exposure happens. The beneficial effect of nanoparticles in improving legume–rhizobia symbiosis should be explored.

Rhizobium in Agricultural Sustainability

Intensive agriculture commonly practiced to meet the food demand of a growing population removes a huge amount of nutrients from the soil. Unless the nutrients are replenished, the agricultural production system will become unsustainable in long run. Legumes, by their symbiotic relationship with *Rhizobium*, fix atmospheric nitrogen and act as a natural fertility restorer. Moreover, nitrogen fixed by rhizobium is more ecologically sustainable. In addition to nitrogen, the bioavailability of many other nutrients also improves due to solubilization and siderophore activity [100]. In addition to their role in nutrient availability, *Rhizobia* also help in biocontrol by antibiosis, parasitism or competition with different pathogens for nutrient uptake [100]. The use of *Rhizobia* can help in reducing the dependence on chemical fertilizers and pesticides to some extent. The practice of *Rhizobium* inoculation for getting can also be integrated into organic farming systems. *Rhizobium* has also been reported to take part in microbe-assisted phytoremediation [100]. The major roles of *Rhizobium* in agricultural sustainability are shown in the following flowchart (Fig. 4).

The application of rhizobium though provides only a part of the nitrogen requirement of the crop need, its role in plant growth promotion cannot be ignored. Moreover, the nitrogen supply by rhizobium when considered on a global basis is huge and when explored properly can reduce the dependence on industrial fixation of nitrogen to a great extent thus reducing carbon footprint. Moreover, the inoculation technology can also be extremely helpful for smallholders and low-income farmers whose purchasing power for fertilizers is relatively lower.

When used in consortia or as a co-culture it can provide multiple ecosystem services in addition to the most popularly conceived role of nutrient addition. The ecosystem services include disease resistance, soil health improvement, stress tolerance to plants, etc. *Rhizobium* technology can also be further improved using biotechnological tools to develop a more effective microbial strain that can perform even better under diverse crop environments and give better results.

Future Thrust

1. The performance of *rhizobium* in the climate change context needs to be evaluated. The negative soil carbon balance, rise in atmospheric carbon dioxide concentration, rise in temperature, etc., are expected to affect legume–rhizobia symbiosis which should be examined. Stress-tolerant strain and their performance should be evaluated under a stressed environment.
2. The nanotechnological interventions in relation to legume–rhizobium interaction are still in a nascent stage. Contrasting results have been reported, which suggest the complexity of nanomaterials–rhizobium–environment–crop interactions. Real-world field-level experiments at multiple locations must study the underlying reasons for such variations
3. Research on better delivery systems, more efficient and stress-neutral strain, and long self-life can be explored for improving the rhizobial performance under varying environment
4. The complex interaction of rhizobium with its partner microorganisms in a consortium must be further studied to understand their behaviour and functioning.

Conclusion

Rhizobium and its role in biological nitrogen fixation is one of the most important biological reactions that contribute to soil fertility and improve crop productivity. Though the *Rhizobium* population may be sufficiently high in areas where legumes are frequently grown, their efficiency in achieving desired nodulation may not be up to the mark due to adverse soil environment, competition from other indigenous microbes, etc. Under such circumstances, inoculation with a suitable *Rhizobia* strain can be effective in achieving a high number of active nodules and more biological nitrogen fixation. Though *Rhizobium*-mediated biological nitrogen fixation is not a new technology, the advancements in the technology need special focus. The advancement of *Rhizobium* inoculation technology especially related to the selection of more efficient strains and the development of advanced formulations has gained attention in the recent past. With the advancement of biotechnology and biochemistry tools, understanding of *Rhizobium* performance and efficiency has been understood better and an attempt has been made to remove the constraints of *Rhizobium* inoculation technology. If *Rhizobium* inoculation technology can

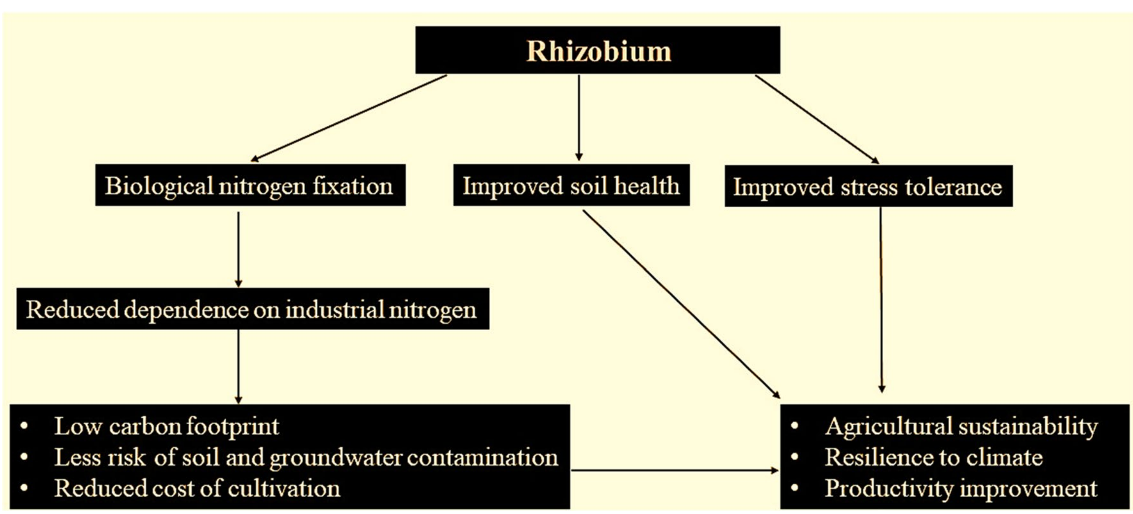

Fig. 4 Role of *Rhizobium* in agricultural sustainability

be exploited to its full potential it can not only reduce the dependence on inorganic fertilizers but also provide additional benefits of crop stress tolerance, improvement in crop growth and better quality of produce.

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Declarations

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