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REVIEW
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Soybean-Nodulating Rhizobia: Ecology, Characterization, Diversity, and Growth Promoting Functions

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The worldwide increase in population continues to threaten the sustainability of agricultural systems since agricultural output must be optimized to meet the global rise in food demand. Sub-Saharan Africa (SSA) is among the regions with a fast-growing population but decreasing crop productivity. Pests and diseases, as well as inadequate nitrogen (N) levels in soils, are some of the biggest restrictions to agricultural production in SSA. N is one of the most important plant-limiting elements in agricultural soils, and its deficit is usually remedied by using nitrogenous fertilizers. However, indiscriminate use of these artificial N fertilizers has been linked to environmental pollution calling for alternative N fertilization mechanisms. Soybean (*Glycine max*) is one of the most important legumes in the world. Several species of rhizobia from the four genera, *Bardyrhizobium*, *Rhizobium*, *Mesorhizobium,* and *Ensifer* (formerly *Sinorhizobium*), are observed to effectively fix N with soybean as well as perform various plant-growth promoting (PGP) functions. The efficiency of the symbiosis differs with the type of rhizobia species, soybean cultivar, and biotic factors. Therefore, a complete understanding of the ecology of indigenous soybean-nodulating rhizobia concerning their genetic diversity and the environmental factors associated with their localization and dominance in the soil is important. This review aimed to understand the potential of indigenous soybean-nodulating rhizobia through a synthesis of the literature regarding their characterization using different approaches, genetic diversity, symbiotic effectiveness, as well as their functions in biological N fixation (BNF) and biocontrol of soybean soil-borne pathogens.

Keywords: biological nitrogen fixation, genetic diversity, rhizobia, soybean, soybean-nodulating rhizobia, soybean root rot pathogens, symbiotic effectiveness

INTRODUCTION

Soybean (*Glycine max*) is among the world's important crops due to its high-quality plant-based protein and oil content (Hartman et al., 2011; Thilakarathna et al., 2019). Worldwide, the crop is grown on about 6% of the arable land (Hartman et al., 2011) and 50% of the legume growing areas (Thilakarathna and Raizada, 2017). Globally, the major soybean-producing countries include the United State of America (USA), Brazil, Argentina, China, and India (Lorito and Woo, 2015). In Africa, different countries, mostly in Sub-Saharan Africa (SSA), grow soybean (Santos, 2019) and the crop is among the most common legumes in SSA (Wilson, 2013; Vanlauwe et al., 2019).

Soybeans establish symbiotic relationships with rhizobia, which form nodules in their roots, leading to biological nitrogen fixation (BNF), or the conversion of atmospheric nitrogen (N_2/N) into biologically active forms that can be used by plants. Rhizobia play a fundamental role in N supply to ecosystems through their ability to fix N in symbiosis with legumes and promote the growth of plants. Through effective symbiosis, annually, soybean can fix about 16.4 Tg of N from the atmosphere which is about 77% of the total amount of N fixed by legumes (Hartman et al., 2011).

Soybean is not a crop of origin in Africa, but the demand is increasing tremendously due to its nutritional value (Chianu et al., 2011; Chianu and Mairura, 2019). Despite the increased demand for the crop, the yield obtained by smallholder farmers is not promising as compared to the major soybean growing areas in the world (Santos, 2019). This needs alternative efforts to increase the productivity of crops while lowering the cost of production, which can be achieved through the use of biofertilizers made from effective rhizobia. Several key joint research projects, such as N_2-Africa, Consultative Group on International Agricultural Research (CGIAR) (Vanlauwe et al., 2019), together with other related research projects on the legume-rhizobium symbiosis, production, and management strategies related to the application of BNF for smallholder farmers in underdeveloped countries, have made the encouraging progress over the previous decade. However, more effort is required for the isolation of effective indigenous rhizobia, commercialization of their biofertilizers, and creation of community awareness for increased and sustainable production of leguminous crops (Ezeaku et al., 2012; Simon et al., 2014; Dawson et al., 2019).

Although the deficiency of nutrients in the soil is reduced by the supplementation of synthetic fertilizers, the productivity of soil and crop yield in SSA are constrained by many factors (Vanlauwe et al., 2011), including poor soil fertility (Vanlauwe et al., 2011; Snapp et al., 2018), and pests and diseases (Tadele, 2017; Franke et al., 2018; Parveen et al., 2019). Low soil fertility in most farming systems is due to inefficient soil management after harvesting crops, which leads to low levels of essential mineral nutrients (Raimi et al., 2017). Soil infertility is also attributed to alkalinity, which covers almost 17% of the arable land in tropical Africa (Ugboh and Ulebor, 2011). N is one of the major plant-limiting nutrients in agricultural soils due to its gradual depletion from the soil due to continuous crop cultivation (Pasley et al., 2019). N deficiency in agricultural soils has increased the demand for chemical nitrogenous fertilizers (Simon et al., 2014). However, chemical fertilizers are known to cause environmental pollution by producing greenhouse gases in the atmosphere, soil, and water pollution through runoff and contaminating the underground water systems through leaching. According to Patel et al. (2017), nitrate pollution of surface waters results in eutrophication and the unsustainability of agricultural production systems. Cognizant of this, there are efforts worldwide to explore alternative methods of N fertilization of crops, especially through the exploitation of legume-rhizobia symbiotic interactions.

Inoculation with rhizobia has been shown to improve N_2-fixation and grain yield in soybean (Rodríguez-Navarro et al., 2003; Fatima et al., 2006; Nyaguthii, 2017; Yuan et al., 2020). However, the effectiveness of newly introduced rhizobial strains is affected by the presence of well-adapted indigenous strains (Burdon et al., 1999; Sannazzaro et al., 2011; Vanlauwe et al., 2019), which may also be inefficient in forming symbiotic nodules with the host plant depending on their N_2-fixing capabilities (Musiyiwa et al., 2005). Among the areas where the soybean crop has been introduced, others have shown poor nodulation reports, which may be due to the absence of effective and compatible N_2-fixing rhizobial strains (Agoyi et al., 2017; Thilakarathna and Raizada, 2017). This calls for a complete understanding of the ecology, genetic diversity, and the environmental factors associated with the localization and dominance of indigenous soybean-nodulating rhizobia. Therefore, this review aims to discuss the potential of indigenous soybean-nodulating rhizobia by synthesizing the literature on their characterization using different approaches, as well as our current knowledge of their genetic diversity, symbiotic effectiveness, BNF and other plant-growth promoting (PGP) functions, and biocontrol of soybean soil-borne pathogens.

CHARACTERIZATION OF SOYBEAN-NODULATING RHIZOBIA

Morphological Characterization

Morphological characterization entails assessing the cultural properties of rhizobial isolates as essential preliminary tools for confirming and distinguishing them from one another. The colony features (macro-morphology), as well as the gram reaction and cell shape (micro-morphology), can be studied for morphological characterization (Singha et al., 2013; Tyagi et al., 2017; Qudratullah Oryakhil, 2020). Macro-morphological features include colony elevation, color, texture, optical density (Kober and Giongo, 2004; Kapembwa et al., 2016; Khansole, 2016; Nagalingam et al., 2020; Qudratullah Oryakhil, 2020), growth rate, production of mucous/exopolysaccharides, elasticity, and pH changes during growth (Ondieki et al., 2017). On the other hand, micro-morphological characterization involves the response to gram stain and the shapes of rhizobial cells (Naz and Bano, 2009). However, molecular approaches can be utilized directly to characterize rhizobia in small samples with narrow diversity, but the morphological characterization is essential in bigger samples and newly isolated rhizobia. **Table 1** shows some morphological features of soybean nodulating rhizobia as described by different studies. The reviewed studies revealed variations in morphological features even for the same species obtained from different locations. Therefore, morphological classification of the newly isolated strains is important in assessing similarities or differences and finally using the information to confirm their identification and classification.

Biochemical Characterization

Biochemical characterization of rhizobia is conducted to test their biochemical features and activities (Singh et al., 2008; Tyagi et al., 2017; Qudratullah Oryakhil, 2020). The biochemical assays are

TABLE 1 | The cultural characteristics of some soybean nodulating rhizobia.

Suspect organism	Colony form	Colony margin	Colony elevation	Colony color	Colony texture	Opacity	Colony growth rate*	References
Rhizobium tropici	Circular, irregular, punctuate	Entire, undulate, lobate	Convex	White, creamy transparent, yellow, pink	Mucoid	Opaque, translucent	Fast	Kapembwa et al., 2016
Bradyrhizobium sp	Circular, irregular, punctuate	Entire, undulate, lobate	Convex	White, creamy transparent, yellow, pink	Mucoid	Opaque, translucent	Slow	Kapembwa et al., 2016
• *Bradyrhizobium japonicum* (5080P) • *Bradyrhizobium japonicum (5080P)*	nt	nt	• Punctiform • Convex high	• nt • nt	• Butirous • Gummy	• Translucent • Opaque	• Slow • Slow	Kober and Giongo, 2004
• *Bradyrhizobium elkanii* ((5019G) • *Bradyrhizobium elkanii* (5019P)	nt	nt	• Convex low • Punctiform	nt	• Gummy • Aqueous	• Opaque • Translucent	• Slow • Slow	Kober and Giongo, 2004
Rhizobium sp	Circular	Entire	Raised	White, creamy, milky	Mucoid	Opaque, translucent	nt	Youseif et al., 2014; Qudratullah Oryakhil, 2020
Mesorhizobium sp	Circular	Entire	nt	Milky, creamy, white	Mucoid	Translucent, opaque	Moderately slow growers	Jida and Assefa, 2012
• *Rhizobium japonicum* • *Currently: Bradyrhizobium japonicum*	Circular	Regular, entire	Convex	Whitish pink and glistering		Opaque	Slow	Khansole, 2016

Fast growers: 2.8–3.8 h, moderate to slow growers: 4.1–5.4 h, Slow growers: 6.4–8.8 h (Odee et al., 1997; Jida and Assefa, 2012), nt, not defined.

conducted for the intended purpose. Some biochemical features of rhizobia tested for various purposes include the reaction of rhizobia to methylene blue and gentian violet treatments. The two dyes are known for their inhibitory effects on the growth of microorganisms, including rhizobia. The results, either positive (+) or negative (-), indicate bacterial growth or no growth, respectively (Wei et al., 2002; Singh et al., 2008). Other important biochemical tests that are conducted include the ability of rhizobia to utilize different carbohydrates as the sole source of energy for their activities. Some carbohydrate utilization assays include hydrolysis of starch, glucose, lactose, sucrose, and citrate hydrolyses (Singh et al., 2008; Khalid et al., 2020).

A gelatine test is conducted by inoculating the rhizobia in a gelatine medium. The degradation of the medium is an indication of the presence of a gelatinase enzyme in the rhizobia (Kumari et al., 2010; Tyagi et al., 2017; Qudratullah Oryakhil, 2020). Production of the gelatinase enzyme by rhizobia is among the features that promote nodulation and N_2 fixation (Kumari et al., 2010; Qudratullah Oryakhil, 2020). Among the products of gelatine hydrolysis by the gelatinase, enzyme are amino acids and peptides. These are the results of reduced inorganic N or fixed N in nodules by rhizobia (Balan et al., 2012). The amino acids produced can also be quantified to determine the amount of N fixed, while peptides can be used as a determinant of interaction between rhizobia and the host plant (Clarke et al., 2014; Tegeder and Masclaux-Daubresse, 2018).

In addition, other biochemical assays conducted to study rhizobia include the urease test, for the determination of the ability of rhizobia to hydrolyze urea into ammonia and carbon dioxide using the urease enzyme (Toffanin et al., 2002). Some rhizobium isolates can grow in urea-supplemented media and change the color of phenol red (a pH indicator) from yellow to pink, indicating that they can secrete urease enzyme (Singh et al., 2011; Mahavidyalaya, 2013). Moreover, Leite et al. (2017) reported on the capability of *Bradyrhizobium yuanmingense* to secrete urease enzyme as an indication of urea hydrolyzation in NH_3 and CO_2 by the strain.

Acidity, alkalinity, and temperature tolerance tests are often conducted to test the adaptation of rhizobia to various edaphic factors (Azcon and Barea, 2010; Deora and Singhal, 2010; Gómez Padilla et al., 2016). Tests for tolerance to acidity and alkalinity are conducted by growing the rhizobia in yeast extract mannitol broth (YEMB) broth or agar medium which is supplemented with Bromothymol blue at different pH at 28°C for 7 days, recording the growth (Maria et al., 2001; Shamseldin and Werner, 2005). For tolerance to acidity, the rhizobia change the green color of the plate to yellow, but for alkaline, the color changes to blue (Shamseldin and Werner, 2005; Kapembwa et al., 2016). Alkaline-producing rhizobia are dominant in acidic soils (Oliveira et al., 2010), while those producing acids dominate alkaline soils (Abd-Alla, 1994; Adhikari et al., 2012; Yan et al., 2014). Soybean nodulating rhizobia such as *Bradyrhizobium liaoningense* and *Sinorhizobium fredii* have been observed to be capable of inhabiting saline-alkaline soils (Wang et al., 2019). Rhizobia use the production of acid or alkaline as an adaptive feature to balance the external environment with their cells. The rhizobia growth can reveal the tolerance of rhizobia to stress conditions when inoculated on YEMB agar medium and kept at lower temperatures of 12, 17, and 25°C (Berrada et al., 2012; Yuan et al., 2020), as well as higher temperatures, such as 37 and 40°C (Maria et al., 2001). Rhizobia having small heat shock proteins (sHSP) are observed to tolerate high temperatures (Nocker et al., 2001; Alexandre and Oliveira, 2013).

Furthermore, an antibiotic resistance test is often conducted to confirm the genus of rhizobia. For instance, *Bradyrhizobium japonicum*-YCK294 was observed to be resistant to Kanamycin (100 μg/ml), Gentamycin (250 μg/ml), 100 μg/ml of Streptomycin and Chloramphenicol, Nalidixic acid (50 μg/ml), Polymyxin B sulfate (50 μg/ml), and Trimethoprim (50 μg/ml) (Sharma et al., 2010). The ability of rhizobia to resist antibiotics increases the chances of their survival in the rhizosphere of plants as well as their ability to occupy a larger number of nodules in symbiotic association with legume plants (Naamala et al., 2016). The summary of antibiotic resistance status for different rhizobia species that have symbiotic associations with soybean is presented in **Table 2**. The biochemical characterization of new strains of isolated rhizobia is important as this will provide accurate biochemical information about the strains and assist in their correct and quick identification. Apart from the importance of biochemical characterization in the identification of soybean rhizobia, it is also worthwhile to conduct various biochemical characterizations for the newly isolated rhizobia species. Biochemical assays such as the growth of rhizobia under different temperature and pH ranges help in the economical and appropriate use of the inoculum based on the climate, soil type, and characteristics under either smallholder or intensive farming.

Molecular Characterization

Many leguminous plant species interact symbiotically with different rhizobia species (Wei et al., 2002; Ojha et al., 2020). However, soybean is among the legumes that nodulate with a narrow diversity of rhizobia. Despite the narrow diversity of rhizobia which forms symbiotic nodules in soybean, the same rhizobia interact with many legumes making the classification a complicated process (Yang et al., 2010; Hayashi et al., 2014; Wang et al., 2018). This requires appropriate molecular methods for the taxonomic classification of diverse rhizobia (Khalid et al., 2020) as well as genes responsible for different functions (Lebrazi et al., 2018). Several molecular techniques used to characterize soybean nodulating rhizobia are discussed hereunder.

Sequencing of the genome and targeted DNA coding regions of interest have been used in classification and studying the diversity of soybean nodulating rhizobia. Sequencing of targeted DNA coding regions involves the use of specific or universal primers and PCR for amplification of the DNA fragment. Different specific or universal primers targeting certain regions or genes of interest in genomic DNA have been used for taxonomic or diversity characterization of indigenous soybean nodulating rhizobia. These techniques include sequencing of DNA coding regions such as 16S rRNA (Chibeba et al., 2017) or both 16S rRNA and 16S rDNA (Youseif et al., 2014; Gyogluu et al., 2018), as well as the 16S-23s rDNA internal transcribed spacer (ITS) region (Htwe et al., 2015). Other markers include enterobacterial repetitive intergenic consensus (ERIC-PCR) (Jain and Pundir, 2017), and repetitive extragenic palindromic (REP; Tajima et al.,

TABLE 2 | Antibiotic resistance and susceptibility of different soybean nodulating rhizobia species isolated from different geographical locations.

***Rhizobia* sp./strain**	**Type of antibiotic***								**References**
	chl	**Eryth**	**amp**	**Kan**	**Neo**	**Str**	**Gent**	**Pen**	
R. fredii	-	-	-	R	S	S	S	R	Scholla and Elkan, 1984
B. daqingense	R	R	-	-	-	-	R	-	Wang et al., 2013
B. diazoefficiens	R	R	R	-	S	S	-	R	Ribeiro and Melo, 2013
B. japonicum USDA 6	R	R	S	-	S	S	-	S	Ribeiro and Melo, 2013
B. huanghuaihaiense	R	R	R	R	R	R	R	-	Zhang et al., 2012
B. liaoningense	R	S	-	-	R	-	R	S	Xu et al., 1995
B. ottawaense	R	R	-	R	-	-	-		Naamala et al., 2016
Rhizobium sp	S	S	R	-	-	-	-	S	Abera et al., 2015
Bradyrhizobium sp	-	R	R	-	-	R	R	R	Abaidoo et al., 2002
Sinorhizobium spp GMR120B	R	S	-	-	-	R	R	R	Temesgen and Assefa, 2020
Mesorhizobium sp	R	-	R	R	-	R	-	-	Benjelloun et al., 2019

*Chl, chloramphenicol; Eryth, erythromycin; Amp, ampicillin; Kan, kanamycin; Neo, neomycin; Str, streptomycin; Gent, gentamicin; Pen, penicillin; Trimeth, trimethoprim; Nalid, nalidixic acid; Polym, polymyxin; Vanc, vancomycin; Nov, novobiocin; R, Resistance; S, susceptibility and (-), not tested.

2000) as well as rep-PCR (BOX) (Chibeba et al., 2017). The aforementioned taxonomic and diversity markers have been used together with other markers for genes with specific functions such as symbiotic genes, which are *nodA* and *nifH* (Youseif et al., 2014), as well as protein-coding housekeeping genes including *dnaK*, *glnII*, *gryB,* and *recA* (Chibeba et al., 2017).

Gyogluu et al. (2018) observed the high genetic diversity of 10 native soybeans nodulating *Bradyrhizobium* strains by characterizing their genomic fingerprinting using ERIC-PCR. Similarly, Tajima et al. (2000) successfully identified and classified 44 *B. japonicum*, 7 *Sinorhizobium meliloti*, and 10 *Rhizobium leguminosarum* in soybean from Japan and Thailand through ERIC-PCR, and REP-PCR, and their combination, ERIC-REP-PCR. Furthermore, ERIC-REP-PCR has been used in the classification of *Bradyrhizobium* in soybean (Chen et al., 2000; Muiru et al., 2010). Chibeba et al. (2017) used rep-PCR (BOX) and 16S rRNA gene sequencing which their phylogenetic study revealed remarkable genetic diversity among *Bradyrhizobium* and *Agrobacterium*/*Rhizobium* species in soybean. Moreover, Wang et al. (2014) identified the high genetic diversity of rhizobia in the rhizosphere of different soybean cultivars by using T-RFLP and 16S rDNA sequencing. Moreover, soybean nodulating rhizobia have been characterized for other functions through a single or combination of various molecular characterization methods. Youseif et al. (2014) successfully studied the genetic diversity of soybean-nodulating rhizobia in Egyptian soils by using rep-PCR fingerprinting and sequencing of symbiotic genes *nifH* and *nodA* and the DNA coding region 16S rDNA.

Other molecular methods have also been used in the characterization of protein-coding housekeeping genes in soybean nodulating rhizobia. Chibeba et al. (2017) used BOX_PCR to amplify the DNA coding region 16S rRNA and protein-coding housekeeping genes, which are *dnaK*, *glnII*, *gyrB*, and *recA*, to characterize indigenous *Bradyrhizobium* strains that were effective in fixing N in soybean. The results from 16S rRNA sequence analysis showed a high nucleotide identity of 97–100% among species, and further characterization of protein-coding genes supported the classification of other five species with those identified through 16S rRNA. This demonstrates the importance of using additional molecular methods in the classification and phylogenetic investigations of soybean nodulating rhizobia.

Genome and targeted DNA (PCR amplicon) sequencing have been used to uncover the microsymbionts of different leguminous plants (Wang et al., 2018). These techniques have been useful in the successful identification of different species of rhizobia from groups/genera which nodulate soybean (Yang et al., 2010; Tian et al., 2012; Wang et al., 2018). Genome sequencing has been used to identify the dominant species in certain biogeographical patterns including edaphic factors such as alkaline-saline soil which was dominated by the genus *Sinorhizobium* in China (Han et al., 2009). Based on the literature, there are various PCR-based procedures, which have been used in studying the taxonomy of soybean nodulating rhizobia for different gene functions. **Table 3** summarizes the genetic diversity of soybean nodulating rhizobia studied in different geographical locations as grouped in their specific genera. Of all the methods, 16S rRNA and16S rDNA are the widely used coding regions for identification, because these are the highly conserved regions existing as multigene families or operons and present in almost all bacteria including rhizobia. Therefore, molecular characterization of newly isolated strains of rhizobia is important in the establishment of the genetic information and characteristics of the organisms.

DIVERSITY OF SOYBEAN-NODULATING RHIZOBIA FROM SINGLE SPECIES *B. JAPONICUM* TO MULTIPLE SPECIES OF RHIZOBIA

Rhizobia is made up of various species that are taxonomically classified as proteobacteria, specifically in the classes α-proteobacteria, which includes many species, and some

TABLE 3 | Genetic diversity of soybean nodulating rhizobia studied in different parts of the world.

Genus	Species	Gene sequenced	Geographical location	References
Bradyrhizobium	• *B. yuanmingense, B. japonicum, B. elkanii, B. liaoningense B. canariense, B. betae* • *Bradyrhizobium sp* • *B. diazoefficiens*	• 16S rRNA, *nifH*, *nodA*, 16S−23S rDNA-ITS region, *nodC*, 16S-23S rRNA- ITS region, *recA, glnII, rpoB, dnaK, atpD, gryB* • Genome, *nodE* and 16S rRNA, |DNA-fingerprint of the SNAP with BOX-A1R primer	• Egypt, India, • Japan, USA, Vietnam, Myanmar, Spain, China, Mozambique	Xu et al., 1995; Saeki et al., 2005; Suzuki et al., 2008; Rodriguez-Navarro et al., 2011; Adhikari et al., 2012; Tian et al., 2012; Shiro et al., 2013; Yan et al., 2014; Youseif et al., 2014; Htwe et al., 2015; Chibeba et al., 2017; Iturralde et al., 2019
*Ensifer (*formerly *Sinorhizobium)*	*S. fredii, S. xinjiangense, S. meliloti S. sojae*	16S rRNA, *nifH*, *nodA*, 16S−23S rDNA, 16S−23S rDNA-ITS, Genome and *nodE*	• Egypt, • Japan, • Vietnam, • China, Spain	Saeki et al., 2005; Suzuki et al., 2008; Rodriguez-Navarro et al., 2011; Tian et al., 2012; Youseif et al., 2014
Rhizobium	• *R. radiobacter, R. rubi, R. vitis, R. undicola, R. rhizogenes, R. leguminosarum bv. Trifolii, R. leguminosarum bv. Viciae* • *Rhizobium sp.*	16S rRNA, *nifH*, *nodA*, 16S−23S rDNA, Genome, *node, glnII, rpoB, dnaK, atpD, gryB,* DNA-fingerprint of the SNAP with BOX-A1R primer	Egypt, China, Mozambique	Tian et al., 2012; Youseif et al., 2014; Chibeba et al., 2017; Iturralde et al., 2019
Mesorhizobium	*Mesorhizobium sp, M. loti, M. tianshanense*	16S rRNA, *nifH*, *nodA*, 16S−23S rDNA, Genome, *node*	Egypt, China, Spain	Rodriguez-Navarro et al., 2011; Tian et al., 2012; Youseif et al., 2014

in β-roteobacteria (Gyaneshwar et al., 2011). There are 17 genera of rhizobia which are categorized into different families (**Figure 1**). The families include *Rhizobiaceae*, *Phyllobacteriaceae*, *Brucellaceae*, *Methylobacteriaceae*, *Bradyrhizobiaceae*, *Xanthobacteraceae*, *Hyphomicrobiaceae,* and *Burkholderiaceae.* Members of the *Rhizobiaceae* include *Rhizobium*, *Ensifer* (formerly *Sinorhizobium*), *Allorhizobium*, *Pararhizobium*, *Neorhizobium*, and *Shinella*. *Phyllobacteriaceae* include *Mesorhizobium*, *Aminobacter*, and *Phyllobacterium*. *Brucellaceae* include *Ochrobactrum*. *Methylobacteriaceae* include *Methylobacterium* and *Microvirga* (Berrada, 2014; Lindstrom and Mousavi, 2020). *Methylobacteriaceae* include *Methylobacterium* and *Microvirga* (Berrada, 2014; Youseif et al., 2014; Jain and Pundir, 2017; Lindstrom and Mousavi, 2020). *Bradyrhizobiaceae* include *Bradyrhizobium*. *Xanthobacteraceae* include *Azorhizobium*. *Hyphomicrobiaceae* include *Devosia.* Finally, *Burkholderiaceae* include *Paraburkholderia* and *Cupriavidus* (Berrada, 2014; Jain and Pundir, 2017; Volpiano et al., 2019; Lindstrom and Mousavi, 2020). However, soybean forms symbiotic nodules with a narrow range of rhizobia species. For a long time, the single species *B. japonicum* was known to accommodate all the strains of rhizobia which nodulate and fix N with soybean. The advancement in DNA sequencing and phylogenetic analyses from different studies revealed that soybean nodulating rhizobia do not fall into the same species due to their heterogeneity. Through DNA homologies, the new species *Bradyrhizobium elkanii* (Hollis et al., 1981; Berrada, 2014) was developed, and hence the third species, *B. liaoningense,* was isolated in China from the soybean nodules. *B. japonicum* and *Bradyrhiszobium elkanii* are categorized as slow growers, but *B. liaoningense* is categorized as a very slow grower (Xu et al., 1995). After the classification of the above three strains, a novel species called *Bradyrhizobium huanghuaihaiense* was isolated in different sites in China (Zhang et al., 2012).

Due to advancements in phylogenetic studies, different soybean-nodulating rhizobia species were classified into other genera, which are *Rhizobium*, *Mesorhizobium*, and *Ensifer*, formerly known as *Sinorhizobium*. The genera *Rhizobium* and *Ensifer* (formerly *Sinorhizobium*), together with the genus *Shinella*, were considered as one branch that included PGPR (Chen et al., 1988; Lajudie et al., 1994). However, due to differences in cultural, biochemical, and molecular characteristics, the genus *Rhizobium* was separated from the genus *Ensifer* (*Sinorhizobium*). Apart from other strains, the soybean nodulating rhizobia such as *R. leguminosarum* (Martinez-romero et al., 1991) were observed to fall under the genus *Rhizobium*. *Ensifer* (*Sinorhizobium*) was then treated as the new genus of fast-growing rhizobia, including those which nodulate soybeans, such as *S. fredii*, *S. meliloti*, and *S. xingianense* (Scholla and Elkan, 1984; Lajudie et al., 1994). The fourth genus of soybean nodulating rhizobia with intermediate growth is *Mesorhizobium*, which was proposed in 1997 (Jarvis et al., 1997). Soybean nodulating rhizobia which were placed in this genus include *M. loti* (Jarvis et al., 1982) and *M. tianshanense* (Jarvis et al., 1997).

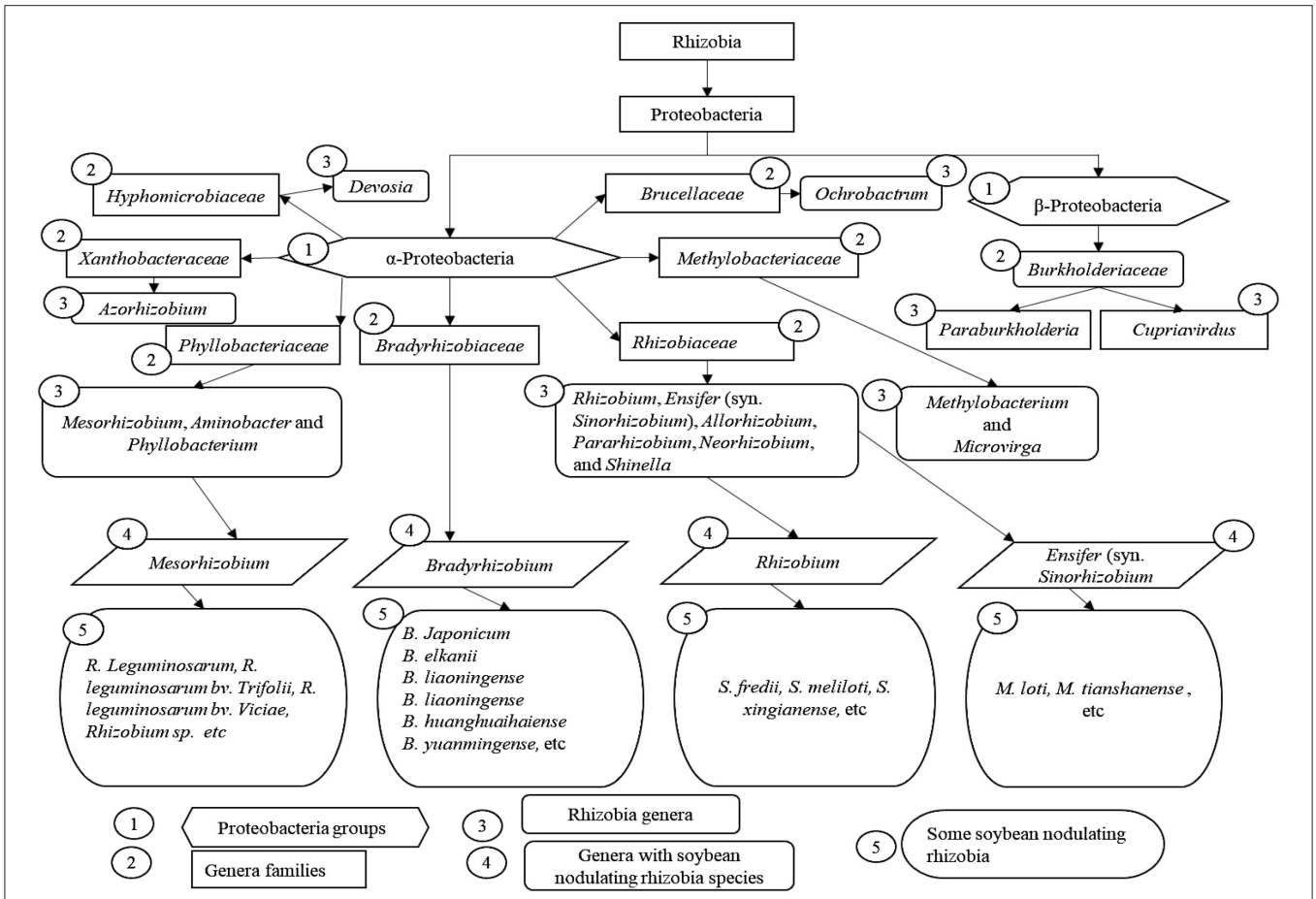

FIGURE 1 | The current classification of soybean nodulating rhizobia.

Through further studies conducted in different geographical locations, different species of soybean nodulating rhizobia have been identified under the four genera (**Table 3**). *Bradyrhizobium japonicum* (Jordan, 1982; Hungria et al., 2001; Musiyiwa et al., 2005; Youseif et al., 2014; Htwe et al., 2019), *B. elkanii* (Hungria et al., 2001; Youseif et al., 2014). *Bradyrhizobium yuanmingense* (Appunu et al., 2008), *B. liaoningense* (Xu et al., 1995), and *R. leguminosarum* (Schaechter, 2009) and later its biovars *R. leguminosarum* bv. *Trifolii*, *R. leguminosarum bv. Viciae* (Tian et al., 2012; Youseif et al., 2014) as well as *R. leguminosarum* bv. *Phaseoli* (Youseif et al., 2014) have been observed to nodulate and fix N effectively in soybean.

The diversity of soybean nodulating rhizobia is affected by host specificity and the narrow range of rhizobia species, which forms an effective symbiosis with soybean (Xu et al., 1995). Climatic conditions and soil properties (Suzuki et al., 2008; Han et al., 2009; Adhikari et al., 2012) and stress conditions such as acidity/alkalinity, salinity, and high temperature (Chibeba et al., 2017) are other factors that affect the effectiveness of soybean nodulating rhizobia. Different land uses and management of crops (Yan et al., 2014), geographical location (Shiro et al., 2013) as well, influence the diversity of soybean nodulating rhizobia. The literature reveals that the rhizobia species which nodulate effectively with soybean are taxonomically placed in four genera, or groups, including *Bradyrhizobium*, *Rhizobium*, *Sinorhizobium*, and *Mesorhizobium*, as summarized in **Figure 1**. Further research is required to explore soybean nodulating rhizobia in regions such as SSA, which currently have inadequate research on BNF studies for different leguminous crops, including soybean. This may be helpful in discovering new rhizobia species capable of forming effective nodules in soybean. Moreover, understanding rhizobial diversity and the associated environmental factors affecting their performance is of paramount importance as, collectively, they affect their distribution in the ecosystem.

EFFECTIVENESS OF INDIGENOUS SOYBEAN NODULATING RHIZOBIA

Most leguminous plants have the capability of associating with symbiotic rhizobia and forming nodules for N fixation (Oldroyd et al., 2011; Mathu et al., 2012). Soybean exhibits a high degree of specificity for effective symbiosis with N fixers (**Figure 2**).

FIGURE 2 | Symbiotic nodules in soybean adapted from Temesgen and Assefa (2020).

Bradyrhizobium is the major symbiont leading to an effective symbiosis with soybean (Merrill et al., 2017; Thilakarathna and Raizada, 2017). *Sinorhizobium fredii* grows fast and has the ability to establish symbiosis for N_2 fixation with soybeans and other legumes (Fan et al., 2017). Although *S. fredii* and other rhizobia can nodulate with a wide range of legumes (Fan et al., 2017), some strains nodulate selectively with a narrow range of legume genotypes or species (Wang et al., 2012).

However, the type of soybean cultivar can affect the effectiveness of nodulation process and N fixation. Effective nodulation depends on plant recognition of Nod factors (NFs) by the host plant (Oldroyd et al., 2011) for the infection of plant roots and nodule formation (Radutoiu et al., 2003; Okazaki et al., 2013). The structural diversity of NFs produced by bacteria is the key determinant of specific symbiotic associations between legumes and rhizobia species (Radutoiu et al., 2007). Some studies have demonstrated the influence of soybean cultivars on the symbiotic effectiveness of the rhizobia species. Wang et al. (2014) observed the influence of soybean cultivars on the composition and diversity of rhizobia in the rhizosphere. The study conducted by Waswa et al. (2014) revealed that the inoculation of soybean seeds by local strain *Bradyrhizobium sp* increased the grain yield from 1.1 to 1.5 t ha^{-1} in promiscuous soybean SB19 and 1.3–1.4 t ha^{-1} in specific a soybean variety (Safari) over the commercial strain USDA110. The difference in yield increase demonstrates the influence of the soybean cultivars in effective nodulation and N fixation as revealed by the variation of seed yield between promiscuous and specific varieties of soybean.

On the other hand, indigenous rhizobia have been observed to be more effective in fixing N than the commercial inoculants which have been previously used in soybean (Musiyiwa et al., 2005; Thuita et al., 2012; Thilakarathna and Raizada, 2017). The study conducted by Ndusha et al. (2019) demonstrated the outperformance of indigenous species of *B. japonicum* over the commercial strain *Bradyrhizobium diazoefficiens* USDA110 by increasing the yield of soybean by 68.7 and 70.8% under greenhouse and field conditions, respectively. Similarly, Chibeba et al. (2017) observed effective nodulation of 85 indigenous soybean nodulating rhizobia isolates under greenhouse conditions, whereby 10 isolates performed better than the best commercial reference strain, *B. diazoefficiens* USDA 110. However, the symbiotic effectiveness of commercial inoculum in soybean can be limited by the presence of indigenous rhizobial strains which are well-adapted and competitive but ineffective in N_2-fixation (Ampomah et al., 2008; Mathu et al., 2012; Kim et al., 2014). Despite the development of promiscuous cultivars that can nodulate with indigenous rhizobial strains (Merrill et al., 2017), it is important to search for indigenous strains that are capable of nodulating a wide range of soybean cultivars. It is also worthwhile to identify the site-specific indigenous soybean nodulating rhizobia to maintain effective nodulation and N fixation. For the improvement of symbiotic interaction between different soybean varieties and rhizobia, it is important to understand the genetic and molecular basis for the host specificity, especially for the new isolates collected from the natural environment.

FACTORS AFFECTING THE EFFECTIVENESS OF BNF IN FARMING AREAS

Temperature Stress

Elevated temperature directly affects the formation and functioning of nodules and, indirectly affects the metabolism of the host plant (Hungria and Vargas, 2000; Aranjuelo et al., 2008). One of the indirect effects of high temperature is the depletion of photosynthetic activity (Long et al., 2004; Islam, 2015) caused by stomatal pores closure (Aranjuelo et al., 2014) under elevated carbon dioxide (CO_2) and temperature (Aranjuelo et al., 2008). Under high temperatures and elevated levels of CO_2, the photosynthetic efficiency of plant leaves decreases, resulting in the inhibition of Rubisco activity, which causes a reduction in N assimilation and reduced carbohydrate concentration in the nodules, resulting in inefficient N fixation (Aranjuelo et al., 2008, 2009). Additionally, high temperatures cause an increased respiration rate, resulting in less substrate availability for the nodules and hence nodule senescence (Hungria and Vargas, 2000; Mohammadi et al., 2012).

Assimilation of N is affected by a decrease in the activities of glutamine synthetase and glutamate synthase (Lea and Miflin, 2018). This results in lower production of allantoin ($C_4H_6N_4O_3$) and allantoic acid ($C_4H_8N_4O_4$), the products of N_2 fixation in root nodules of soybean and other tropical and sub-tropical legumes (Bikash et al., 2016; Liu et al., 2018) are transported to the shoot *via* xylem vessels (Ono et al., 2021). At a root level, elevated temperature affects N_2 fixation by decreasing the formation of root hairs, reducing the sites of nodulation, and altering

bacterial adherence to root hairs (Hungria and Vargas, 2000; Aranjuelo et al., 2007; Mohammadi et al., 2012). Additionally, high temperature affects molecular signals exchange between the host plant and rhizobia through a decrease in nod-gene inducers (Mabood and Smith, 2005; Mohammadi et al., 2012).

Other factors that are mostly affected by high temperatures include root infection, nodule initiation, and nodule function. Under high-temperature conditions, the survival of rhizobia in the soil is reduced, genetic modification or loss of plasmid occurs, as well as the poor physiological state of surviving rhizobia leading to failure of them to infect root hairs. For the host plant, under high temperatures, the physiological activities are affected, and the development of roots is reduced, resulting in reduced infection sites and leading to failure of nodule initiation. The exchange of molecular signals, especially *nod* factors and signaling compounds such as flavonoids, between host plants and rhizobia is also affected by high temperature (Hungria and Vargas, 2000; Miransari and Smith, 2009; Mandal et al., 2010; Mario et al., 2015).

However, some soybean nodulating rhizobia have been observed to tolerate high-temperature conditions. Yuan et al. (2020) found that 13 out of 77 isolates of soybean nodulating rhizobia were able to grow under a high temperature of 44°C. Through the phylogenetic analysis, the strains were observed to fall within the *Bradyrhizobium* and *Rhizobium* genera. Similarly, Asadi et al. (2009) isolated 56 *Bradyrhizobium sp* from soils and tested them in an *in vitro* environment for their ability to tolerate higher temperature conditions, finding that 19 isolates could grow at 38°C and 10 at 41°C. For the effectiveness of N fixation in areas with high temperatures, it is important to isolate the well-adapted indigenous soybean nodulating rhizobia for commercialization.

Soil Moisture Content

Moisture availability of the soil is determined by soil moisture-retaining capacity (Hungria and Vargas, 2000). Moisture stress in the soil results in the reduction of nodule weight and nitrogenase activity and hence affects the N_2 fixation process (Siczek and Lipiec, 2011; Dabessa et al., 2018; Santachiara et al., 2019). Although some rhizobial populations occur in desert soils and are effective in nodulation, viable strains cannot survive or function under high moisture stress (Lucrecia et al., 2003; Bashan et al., 2014; Dabessa et al., 2018). Drought is among the major environmental stresses which affect the survival of N_2-fixing bacteria and the nodule initiation stage because plants need more adequate moisture during this stage than other stages (Monica et al., 2013). Furthermore, some studies bio-prospect the tolerance of some rhizobial strains under moisture deficiency.

Mnasri et al. (2007) observed that *Ensifer meliloti* bv. *Mediterranense* 4H41, a salt-tolerant strain was highly competitive and effective in nodulating common bean (*Phaseolus vulgaris*) under conditions of water scarcity. Through PCR-RFLP of 16S rRNA and *nodC,* the same study revealed that drought stress narrows the genetic diversity of nodulating rhizobia. Similarly, Hungria and Vargas (2000) reported the ability of *Rhizobium tropici* to fix N under water stress conditions. Rampa et al. (2019) found that the soybean nodulating *Bradyrhizobium diazoefficiens* was capable of fixing N under drought conditions. Similarly, Kunert et al. (2016) reported the ability of *Bradyrhizobium sp* to form an effective symbiotic association with soybean under water deficit conditions. The consortium of *B. japonicum–Trichoderma Harzianum* is also observed to increase the productivity of soybean under drought conditions (Nahrawy et al., 2020). More research is needed to investigate the capabilities of indigenous soybean nodulating on N fixation in drought environments, as well as the survival rates of the cells in the soil.

Soil Acidity, Alkalinity, and Salinity

Soil pH determines the availability of nutrients for plant uptake in the soil (Roem and Berendse, 2000; Stark et al., 2012; Penn, 2019). Soil phosphorus (P), acidity, alkalinity, and salinity are among the abiotic factors which determine biogeographical patterns of soybean nodulating rhizobia (Han et al., 2009, 2020; Zhang et al., 2018). The rhizobia population and activities vary among different soil conditions. P is a very important nutrient in the symbiotic association process as it is involved in plants' energy (ATP) acquisition, storage, and utilization (Mmbaga et al., 2014). Iron (Fe) and aluminum (Al) abundance in acidic soil, as well as calcium (Ca) and magnesium (Mg) abundance in alkaline soil, fix soil P in the form of oxides and hydroxides, rendering P unavailable for plant uptake (Dabessa et al., 2018).

Acidic soil causes root injury, leading to reduced water and nutrient uptake as well as endangering the survival of soil microorganisms (Kidd and Proctor, 2001). Furthermore, soil acidity has been observed to negatively affect the process of BNF by altering cell-membrane permeability caused by excess $H,^{+}$ which induces cation efflux and hence impairing nutrients availability to plants (Ferreira et al., 2016). Alkalinity in soil reduces the abundance, activities, and diversity of rhizobia (Li et al., 2011a,b; Zhang et al., 2017, 2018).

Both extreme soil acidity and alkalinity affect the activities of rhizobia in the soil by inhibiting the growth and the process of nodule initiation (Slattery et al., 2001; Azcon and Barea, 2010; Gómez Padilla et al., 2016). The *nod* genes of rhizobia are suppressed, the rate of multiplication of rhizobia and root infection is reduced, the distribution and recolonization of the soil are also restricted (Slattery et al., 2001; Miransari and Smith, 2009; Mario et al., 2015). Studies have reported a few species of soybean nodulating rhizobia are tolerant to abiotic stresses. *R. tropici* and *Bradyrhizobium sp.* are tolerant to soil acidity (Graham et al., 1994) and *B. liaoningense* and *B. yuanmingense* species are tolerant to soil alkalinity (Gómez Padilla et al., 2016).

Tian et al. (2012) conducted a study on the comparative genomics of soybean nodulating rhizobia *Bradyrhizobium* and *Sinorhizobium* for gene adaptations to acidic, neutral, and saline-alkaline soils. The results demonstrated clear biogeographic patterns that *S. fredii* dominated in alkaline-saline soil, while *Bradyrhizobium* species dominated in neutral to acidic soil. Several other studies have also confirmed that genus *Sinorhizobium* are dominant in alkaline–saline soils, whereby those which are *Bradyrhizobium,* dominate neutral to acidic soils (Li et al., 2011a; Zhang et al., 2011, 2017, 2018), observed *S. sojae* as soybean microsymbionts that inhabit the regions of

alkaline soils. Therefore, for the effective symbiosis of indigenous rhizobia that nodulate soybean, it is important to explore the biogeographic patterns, underlying effective nodulation.

Macronutrients

Nitrogen

Nitrogen is the most limiting essential nutrient for plant growth and development (Pasley et al., 2019). The element partakes in numerous metabolic pathways as well as in the synthesis of molecules such as proteins (Bruijn, 2015), nucleic acids, hormones, and chlorophyll (Saturno et al., 2017; Dabessa et al., 2018). Various sources of N in the soil include mineralized organic matter (Ray et al., 2006; Salvagiotti et al., 2008; Ramakrishnan, 2015), BNF, industrial chemical N fertilizers (Ramakrishnan, 2015), lightning, volcanism, and combustion of fossil fuels (Saturno et al., 2017). High levels of N in the soil or that from inorganic fertilizers are reported to inhibit the growth of soil rhizobia (Dabessa et al., 2018), nodule formation, Nase activity, reduce infection threads (Liu et al., 2009; Guan et al., 2013; Saturno et al., 2017), and hence limit N_2 fixation (Weisany et al., 2013; Dabessa et al., 2018). When the level of mineral N is higher in the soil, the plants use lesser energy to take up N from the soil than through fixation, hence shifting from symbiotic to inorganic N nutrition (Liu et al., 2009). In legume production, inorganic N is required during the N hunger period for the healthy growth of plants, which facilitates nodule formation (Marino et al., 2013). The study conducted by Kassam (2019) and Wang et al. (2020) revealed that higher levels of N in the soil from supplementation by industrial fertilizers affected the nodulation efficiency of *Bradyrhizobium sp* with soybean.

Phosphorus

Phosphorus is an important essential nutrient element in the N_2-fixation process as it is involved in the plants' energy acquisition, storage, and utilization for the N_2-fixation process (Mmbaga et al., 2014). The availability of P results in an increase in the number, size, and weight of nodules (Abebe, 2017). Inadequate levels of P in the soil inhibit symbiotic association between plants and rhizobia, reduction in the mass of nodules, N_2-fixation, as well as the yield of leguminous crops (Abebe, 2017; Dabessa et al., 2018). Unavailability of P for plants' uptake may be due to extreme soil pH. Under extreme acidity, P is adsorbed or held in active sites of the soil particles surfaces (Idris and Ahmed, 2012; Mbene et al., 2017). In acid soils, P reacts with oxides and hydroxides of Fe and Al, while in alkaline soils, P reacts with the oxides and hydroxides of cCa (Dabessa et al., 2018). Under such conditions, nodulation and N fixation are inhibited.

Some N-fixing bacteria through interaction with legumes such as soybean are capable of solubilizing P in soil and increasing P use efficiency by plants as well as facilitating the BNF process (Drevon and Abadie, 2015). Mallaiah (2009) observed the ability of *Rhizobium* isolates/strains from different legumes to solubilize P from different compounds. The study conducted by (Fatima et al., 2006) demonstrated that *Rhizobium* strains capable of nodulating soybean can solubilize P in the soil for utilization by plants. Similarly, Igiehon et al. (2019) investigated the capability of soybean nodulating *Rhizobium sp*, *Rhizobium tropici*, *Rhizobium cellulosilyticum*, *Rhizobium taibaishanense,* and *Ensifer meliloti* in solubilizing P in the soil. Among the five strains, *Rhizobium tropici* exhibited the bigger halo-zone of 17.3 mm in pikovskaya's agar medium whereby the smallest diameter of halo-zone (10.7 mm) was exhibited by *Ensifer meliloti*. From the study, the author declared that all five strains of *Rhizobium* possess the traits of phosphate solubilization. Therefore, as phosphorous is an important element in numerous molecular processes in N fixation, its availability is crucial in the establishment of the symbiotic relationship between the host legume and rhizobia.

Potassium and Sulfur

Symbiotic organisms, including rhizobia, are sensitive to low levels of K when compared to their leguminous host plants. Conversely, potassium ion (K^+) plays a significant role as an osmolyte for adaptation in saline soils. Irrigation triggers salinity problems in soils. To ensure the suitability of irrigated soils for cultivating symbiotic legumes, the levels of exchangeable K^+ need special consideration (Bonilla and Bolaños, 2009; Wakeel et al., 2011). K is important in the uptake of water and growth of roots in plants, and these influence the nodulation process by increasing the nodulation sites (Youssef et al., 2001; Mfilinge et al., 2014). Studies have reported improved N fixation in the presence of K (Sherwood, 1970).

On the other hand, sulfur (S) is an essential nutrient for plant growth and development. However, the nutrient has received little attention in BNF research, despite the fact that plants that rely on N fixed by rhizobia require more S than plants that rely on mineral N supplements (Divito and Sadras, 2014). S is essential for buffering soil alkalinity and improving rhizobia activities by increasing the number of nodules, N_2 fixation, and thus legume yield (Anandham et al., 2007). Some studies have shown that S deficiency lowers BNF because of reduced nodule development as well as Nase and leghemoglobin. The reduction of nodule development, nitrogenase, and leghemoglobin is caused by the N-feedback mechanism, which has been demonstrated to reduce the absorption of mineral N. When the absorption of mineral N is reduced, the fate is the prolonged reduction of N-assimilation, uptake, and fixation by plants in S-deficient soils. This is due to increased levels of N-rich amino acids, especially asparagine, which are responsible for feedback inhibition of N-assimilation. The same study has demonstrated the increase of N-concentration in the nodules as well as N-absorption and fixation upon sulfate application (Varin et al., 2010). The study conducted by Getachew et al. (2016) revealed that the application of S in soil resulted in the improvement of N fixation, improved plant growth, and nutrient uptake by rhizobia inoculated soybean. Similarly, Weisany et al. (2013) observed less growth of *Bradyrhizobium sp* in media supplemented with a low concentration of S, indicating that S is a very important nutrient for effective nodulation. More studies are required in the roles of K and S on N fixation for the new strains to be identified.

Calcium

Calcium is one of the secondary macronutrients in the soil (Dar et al., 2014). Amongst its roles in plant growth, Ca is

essential in the development of plant roots (Hepler, 2005). In the symbiotic association between leguminous plants and rhizobia, Ca enhances the attachment of rhizobia to root hairs, infecting the root and hence nodulation (Dabessa et al., 2018). High levels of Ca in the soil enhance the higher abundance of rhizobia which results in a higher number of nodules in leguminous plants (Bonilla and Bolaños, 2009). The essentiality of Ca in early infection events (El-Hamdaoui et al., 2003) is an indication that the ion is important in plant-bacteria signaling and recognition of nod factors from rhizobia. The activity of *Nod* genes increases with the levels of Ca in soil being higher (CapoCapoen et al., 2009). This is because, Ca increases the levels of flavonoids in plant root exudates, and the flavonoids are responsible for the induction of nod genes due to signal perception by rhizobia (Miwa et al., 2006). Ca in plants enhances the activity of phenylalanine ammonia-lyase which is the key enzyme responsible for the pathway of flavonoids synthesis (Debona et al., 2017).

The presence of Ca ions enhances bacterial exopolysaccharides in forming a gel as a device for rhizobia to attach to root hairs. Ca strengthens the activities of plant-binding proteins (lectins) as well as rhizobial Ca-dependent adhesion by acting as a ligand (Bonilla and Bolaños, 2009; Janczarek et al., 2015). This signifies that Ca is essential for the optimal colonization of root hair by rhizobia (Fauvart and Michiels, 2008; Abdian et al., 2013).

Concerning the importance of Ca ions in root hair development and infection interactions, the spiking of Ca^{2+} is crucial in the transduction of signals during the perception of NFs and the organogenesis of nodules. Ca has been revealed as a second messenger in NFs signal transduction following its detectable effect of influx at the root hair tip leading to efflux of chloride ions (Cl^-) and hence membrane depolarization (Cullimore et al., 2001; Oldroyd and Downie, 2004; Crespi and Frugier, 2009). The influx of Ca^{2+} in the root hair tip results in Ca oscillation in the root hair zone. This has been observed to facilitate faster nodulation than the normal invasion of root hair by rhizobia. Rhizobia can enter into their host through cracks formed during lateral root development, but this has been observed to be associated with the death of cells responsible for the formation of infection pockets (Cullimore et al., 2001). At the root hair tip, Ca becomes one of the aqueous components of the cell cytoplasm. The dynamics of Ca may be related to the infection events such as the swelling of root hair tip, vacuolation, and alignment of endoplasmic reticulum with the plasma membrane, movement of nuclear to the swelling root hair, and the inner growth of the cell wall for the initiation of infection threads (Bonilla and Bolaños, 2009). More studies are required on the role of Ca in influencing the activities of isolated but uncharacterized indigenous rhizobia that nodulate and effectively fix N with soybean.

Magnesium

Magnesium is required by rhizobia to stabilize cell membranes, nucleic acids, and ribosomes and has an important role as an enzyme cofactor. Mg serves as a cofactor for many enzymes, complexes with ATP, and has key roles in stabilizing ribosomes and cell walls. Mg-deficient cells of some gram-negative bacteria are very sensitive to environmental stress such as drought and die very quickly (O'Hara, 2001). In biological N fixation, Mg influences nodule formation (Kiss et al., 2004; Ramesh and Winkler, 2010). It is an important nutrient element in the process of photosynthesis as it is involved in enzymatic reactions, enabling them to perform properly, including urease and nitrogenase, which are involved in N fixation (Cakmak and Yazici, 2010; Gransee and Führs, 2013). Mg is reported to be important in the metabolism of rhizobia by facilitating the alteration of carbohydrate partitioning and transport into nodules (Peng et al., 2018). Some reports revealed that the addition of Mg together with other nutrient elements contributed to an increase in nodulation as well as the yield and quality of soybean seeds inoculated with *Bardyrhizobium sp* (Okereke and Onochie, 1996; Masunga et al., 2016). Similarly, Khaitov (2018) found a significant increase in the shoot and root biomass pod numbers as well as increased Mg levels in the nodules upon the addition of optimum levels of Mg and inoculation by *Bradyrhizobium sp*. To investigate the further roles of Mg on nodulation and plant growth and development, it is important to test the effects of Mg and inoculation of soybean seeds with different species of newly isolated indigenous rhizobia that effectively fix N with soybean.

Micronutrients

Iron (Fe) and Molybdenum (Mo)

Iron and Molybdenum are the important micronutrients in nitrogenase enzyme activities and cofactors. The two nutrients are the major components of the nitrogenase enzyme system (Bonilla and Bolaños, 2009), which are MoFe protein (MoFe heterotetramer) products of *nifDK*, Fe-protein a product of *nifH* which is an oxygen-sensitive metalloenzyme complex, and molybdenum-nitrogenase encoded by *nifHDK* (Boyd et al., 2011). The *nifH* genes are responsible for the encoding of nitrogenase enzyme activities. Iron is a cofactor for other proteins inside the nodule which are important in N_2-fixation, including leghemoglobin, cytochromes, or ferredoxin (Bonilla and Bolaños, 2009). Fe and Mo at optimum levels in the soil were demonstrated to elevate the concentration of N, proteins, and leghemoglobin in *Cicer arietinum* Land *Vigna radiata* (L) (Khan et al., 2014a; Lalita and Kumar, 2017). Between these two nutrients, Mo availability is also hindered by the acidity in the soil as well as the acidifying effect of nitrogenase activity (Doerge et al., 1985). Moreover, Mo is crucial in plant N uptake and N fixation due to the activities of nitrate reductase and nitrogenase enzymes for which Mo acts as a co-factor (Mendel, 2013; Oburger et al., 2018). Therefore, the supply of Fe and Mo is very important for nodulation and N_2-fixation. For these reasons, the supplementation of soils with optimum levels of these nutrients can improve the BNF process in legumes as well as increase yield (Bonilla and Bolaños, 2009; Khan et al., 2014a). Rotaru and Sinclair (2009) found that higher levels of iron in the nodules resulted in a significant increase in the N fixation rate and export of ureides from the nodules to the leaves of soybean inoculated with *B. japonicum*. Bambara and Ndakidemi (2010) reported that the application of Molybdenum significantly

improved the symbiotic performance of a leguminous crop in the field.

Copper (Cu) and Cobalt (Co)

Copper (Cu) and Cobalt (Co) has been demonstrated to be involved in the synthesis of leghemoglobin in the nodules due to the presence of vitamin B_{12}, whose concentration in the pinkish nodules is higher as compared with white nodules. The increase in the size of nodules with the increasing levels of Co while Cu has been observed to increase the concentration of N and yield of subterranean clover (Hallsworth et al., 1960; O'Hara, 2001). The study conducted by Wahab et al. (1996) demonstrated the contribution of Cu and Co to nodulation and yield parameters of faba beans. Cobalt was observed to increase the number and weight of nodules while Cu increased the nodule mass. Both metals were observed to increase nitrogenase activity, leghaemoglobin content, dry matter, and total N content of shoots and roots. In the differentiation of bacteroids, Co is essential in the endoreduplication of rhizobia due to its composition in ribonucleotide reductases (Ronald, 2011). Copper ion is also observed to be responsible for the transduction of ATP/energy in microaerobic environments (González-Guerrero et al., 2014).

Nickel (Ni), Manganese (Mn), and Zinc (Zn)

Nickel (Ni) has been indicated as an important metal in BNF due to its significance in the expression and biosynthesis of hydrogenase enzyme (Lavres et al., 2016) which recycles the H_2 produced during N_2–fixation to conserve energy (González-Guerrero et al., 2014). Ni has been noticed to increase the growth of rhizobia on yeast extract mannitol and the minimum medium with glutamate as an N source. At optimum concentration, Ni is reported to contribute to the increase of the number of nodules, the activity of nitrogenase enzyme, and the plant dry weight in pigeon pea and green gram (Singh and Rao, 1997). According to Lavres et al. (2016), the optimum levels of Ni have significant importance in BNF as they relate to N of N uptake, activities of Nase and urease enzymes, nodulation, plant, and grain dry matter yield of soybean. The recommended concentrations of Mn and Zn should be used to avoid their toxicity and inhibition of rhizobial growth (Wilson and Reisenauer, 1970). More studies are required on the physiological roles of Ni, manganese (Mn), and zinc (Zn) in biological N fixation.

For effective BNF in soybeans and other legumes, it is critical to understand soil characteristics such as soil type, nutrient levels, and climate, particularly temperature and moisture content. Another very important factor is the assessment of soil acidity, alkalinity, and salinity, which are determined by soil pH. *In situ* trials in different soil types and conditions for the commercial inoculants, which are made from the newly isolated and identified rhizobia, are very important so as to avoid uneconomical and inappropriate use under various soil types. It is also worth isolating site-specific rhizobia species, which can form effective symbioses, especially for problematic soils such as acidic, alkaline, and saline soils as well as extreme temperatures and drought. Considering all these factors will help to avoid compromising the effectiveness of rhizobia inoculants and also ensure the economical and appropriate use of inoculum for smallholder farmers as well as under intensive farming.

PLANT GROWTH-PROMOTING FUNCTIONS OF SOYBEAN-NODULATING RHIZOBIA

Apart from the main and most commonly referred to PGP role of rhizobia, BNF, rhizobia possess other PGP traits such as nutrient solubilization such as P, K, and Zn solubilization, as well as siderophore production for iron solubilization. Others include the production of phytohormones such as indole-acetic-acid (IAA) (Igiehon et al., 2019; Aloo et al., 2021), exopolysaccharide (EPS), 1-aminocyclopropane-1-carboxylate (ACC) (Igiehon et al., 2019), cytokinins, gibberellins, riboflavin, and lumichrome (Jaiswal et al., 2021). Apart from promoting the growth in soybean as its symbionts, some species of soybean nodulating rhizobia promote the growth in non-leguminous plants directly or indirectly. Among others, some of the PGP functions in non-leguminous plants such as the production of Abscisic acid (ABA) by *Bradyrhizobium japonicum* USDA110 along with gibberellins, can serve the purpose of alleviating water stress in maize plants. The nutrients solubilized and released in soil solution for instance P (Khan et al., 2014b), K (Kalkar, 2014; Choudhary et al., 2018; Sattar et al., 2019), and Zn (Rani et al., 2020) available for uptake by all plants including non-leguminous plants. For this review, four of the PGP functions, including BNF, nutrients solubilization, siderophore, and indole-acetic-acid (IAA), will be discussed hereunder.

Biological Nitrogen Fixation

Like all other symbiotic associations with leguminous plants, biological N_2 fixation is the most important function of soybean nodulating rhizobia. Biological N_2 fixation is an inexpensive and environmentally-friendly alternative source of N_2 in which atmospheric N is transformed into biologically active N that can be utilized by plants (Bhattacharjee and Dey, 2014; Simon et al., 2014; Gupta et al., 2015; Suhag, 2016). Symbiotic N_2 fixation plays a central role in the production of a million tons of total biological N. The significance of these microbes is evident from the fact that although a total of 100 million metric tons of synthetic N is produced per year, N_2 fixing microbes convert about 200 million tons of N to ammonia yearly (Glazer and Nikaido, 2007). The study conducted by Nyaguthii (2017) found that the inoculation of soybean by rhizobia made the grain yield up to 2 tons per hectare. Similarly, Heerwaarden et al. (2017) found that in Sub-Saharan Africa, the inoculation of soybean seeds with rhizobia increased the yield from 1,227 to 1,343 kg/ha in field trials conducted from 2010 to 2015.

Phosphate Solubilization

Phosphorus is the second essential and limiting nutrient element in the soil after N. In soil, the availability of P is rarely adequate for satisfying the plants' requirements due to its fixation in oxides or hydroxides of aluminum/iron or Ca/Mg in the soil, hence unavailable for plant uptake. It is estimated that the deficiency

of P in soil reduces the yield of crops by 30–40%, which leads to excessive application of P fertilizers (Malhotra et al., 2018). In soil, the concentration of P is about 2×10^3 higher than the amount required by plants, but only 15–20% is available for plants' uptake while the rest remains unavailable and leaches to surface and groundwater, leading to eutrophication (Smith et al., 2000). For the P to be available to plants, it must be in soil solution in the form of soluble P. Solubility of P in the soil can be increased by plants through exploration of nutrients by roots and exudates such as organic anions and phosphatases (Richardson et al., 2009). For the P to be available in the soil solution, it has to undergo the processes of solubilization and mineralization for inorganic and organic P, respectively, influenced by the microbial and physicochemical structure of the soil as well as plant exudates (Khan et al., 2014b).

Phosphate solubilizing organisms use the same approach of solubilizing insoluble P compounds such as tricalcium phosphate $(Ca_3PO_4)_2$, aluminum phosphate (Al_3PO_4), iron phosphate (Fe_3PO_4), and others, hence making them available for uptake by plants (Gupta et al., 2007). Phosphate solubilizing microorganisms secrete low molecular mass organic acids (OA), which chelate with mineral ions and hence release P in the soil solution. Inorganic acids such as HCl, HNO_3, and H_2SO_4 are also documented as another mechanism used by PS microorganisms to chelate mineral ions and release P in soil solution (Khan et al., 2014b). Another mechanism used by microbes is the secretion of enzymes, such as phosphatase and phytases (Maougal et al., 2014), which converts organic P to inorganic form, which is also available for uptake by plants (Yadav and Tarafdar, 2003; Maougal et al., 2014). Several types of bacteria, including rhizobia in the soil, can solubilize a high proportion of P (Elkoca et al., 2008; Collavino and Sansberro, 2010; Kapri and Tewari, 2010; Hajjam and Cherkaoui, 2017). *Bradyrhizobium sp* (Mahavidyalaya, 2013) and *B. japonicum* (Wasule et al., 2003), which nodulates soybean, are capable of solubilizing P. Therefore, apart from the main role of fixing N in the soil, rhizobia can serve the dual purpose of fixing N, solubilizing P in the soil, and hence reducing the excessive application of synthetic fertilizers such as phosphates. It is worthwhile to investigate new rhizobia species that are successful in P solubilization, especially in difficult soils such as acidic, alkaline, and saline soils, where P is fixed in the oxides and hydroxides of Fe, Al, Ca, and Mg and therefore unavailable for plant uptake.

Potassium Solubilization

Potassium is the third macronutrient, following N and P. Its importance is increasing significantly due to increased requirements caused by its continuous production of crops (Dotaniya et al., 2016; Choudhary et al., 2018). Although the element is abundant in soil, it is less available for uptake by plants (Bhattacharyya et al., 2016). This is due to fixation in the soil where almost all K remains as insoluble rocks, necessitating a large reliance on synthetic fertilizers to meet plant requirements (David, 2010; Yadegari and Mosadeghzad, 2012; Choudhary et al., 2018). In the soil, microorganisms including rhizobia (Sessitsch et al., 2013) use organic ligands, enzymes, hydroxyl anions, and biofilms to solubilize K from the minerals such as mica, illite, biotite, and muscovite (Das and Pradhan, 2016) and hence contribute to the availability of the nutrient for uptake by plants (Alikhani, 2017). The process of K solubilization by bacteria involves acidolysis, chelation, complexolysis, and exchange reactions (Kalkar, 2014; Choudhary et al., 2018; Sattar et al., 2019). However, the effectiveness of bacteria to solubilize K depends on the type of soil, bacterial strain, and the form of insoluble K. Some rhizobia, which fixes N in leguminous plants, have been observed to solubilize K in agricultural soils. This is drawing attention to the aspect of sustainability in cropping systems by increasing the availability of K in agricultural soils through a sustainable and reliable source but also environmentally friendly (Meena et al., 2015). According to a study by Htwe et al. (2019), inoculation of soybeans with a combination of *Bradyrhizobium sp* and *Streptomyces griseoflavus* increased K uptake at three unfolded trifoliate leaves (V3) in Japan soybean varieties, and at V3 and R2 (full bloom) in Myanmar soybean varieties. This indicates that the two bacteria have a greater ability to solubilize K when inoculated together. *Sinorhizobium meliloti* one of the soybean nodulating rhizobia have been reported to solubilize K (Deshwal, 2020). With regard to the above studies revealing the capabilities of some soybean nodulating rhizoa in solubilizing K, more research is needed to explore diverse indigenous soybean nodulating rhizobia that are effective in solubilizing K, in order to develop a biofertilizer that will reduce deficiency while also ensuring a sustainable and environmentally friendly supply of K in agricultural soils.

Zinc Solubilization

Zinc is among the seventeen essential plant nutrients in which it is a micronutrient (Mousavi et al., 2013). In agricultural soils, the deficiency of Zn is reduced by supplementation of synthetic fertilizers such as $ZnSO_4$, $ZnNO_3$, ZnO, $(ZnCl_2)$, or $ZnCO_3$ to meet crop requirements. However, a greater proportion of the supplemented Zn (Mclaughlin, 2014) is fixed to insoluble complexes (zincate) especially alkaline soils (Udeigwe et al., 2016). This makes it unavailable for uptake by plants (Mclaughlin, 2014; Hacisalihoglu, 2020). In soil, Zn solubilizing bacteria (ZNB) produce organic acids such as gluconic and ketogluconate, which combine with soil mineral surfaces and form compounds with Zn and hence chelation of Zn through carboxyl and hydroxyl groups, which then facilitate the solubility of Zn (Rani et al., 2020). Some non-rhizobia endophytic bacteria (NREB), in soybean nodules, *Pseudomonas sp* have been observed to solubilize Zn under *in vitro* conditions and their synergistic effect with N_2 fixing rhizobia promotes the growth of soybean plants. Poonam et al. (2019) demonstrated that NREB has a good ability to solubilize Zn and the synergistic effect of *Bradyrhizobium sp* (LSBR-3) and NREB, *Pseudomonas aeruginosa* (LSE-2) improved the growth of soybean plants as compared to inoculation by *Bradyrhizobium sp* (LSBR-3) alone and non-inoculated treatment. Similarly, (2014) conducted a co-inoculation study of soybean seeds with *B. japonicum* and each of *Nocardia alba* S4301, *Nonomuraea rubra* S3304, and *Actinomadura glauciflava* significantly increased the yield of soybean as well as nutrients concentration including Zn in plant samples. However, there is limited information about the

solubilization of Zn by soybean nodulating rhizobia. Therefore, isolation of diverse soybean nodulating rhizobia from different soil types to obtain the effective species with the dual purpose of fixing N and Zn solubilization or a consortium inoculation to save both purposes is important for sustainable availability of Zn to plants in agricultural soils.

Siderophore Production

Iron (Fe) is an important nutrient in the BNF process as it is a co-factor of leghemoglobin, cytochromes, ferredoxin (Bonilla and Bolaños, 2009), and nitrogenase enzyme (Paudyal et al., 2007). Although Fe is adequate in most soils, its substantial amount is inaccessible to plants due to the low solubility of its oxides, making Fe deficient in many agricultural soils (Colombo et al., 2014; Arora and Verma, 2017). Siderophores are low-molecular-weight secondary metabolites that chelate with iron (Arora and Verma, 2017). Siderophores are unique compounds with functional groups and electron-rich side chains (Verma et al., 2011; Ghavami et al., 2017) that bind ferric ions and transport them across the cell membrane (Niehus et al., 2017). In soils with inadequate iron, bacteria, including rhizobia, produce siderophores, which chelate the iron and subsequently solubilize it into complexes that are easily available for uptake by plants (Mathew et al., 2014; Boiteau et al., 2016). The ability of microorganisms to produce siderophores can be a sustainable solution to making iron readily available for uptake by plants in iron-deficient soils. Catecholates, carboxylates, hydroxamates, and combinations of these are produced by a variety of bacteria, including rhizobia (Anastasiou et al., 2014; Mimmo et al., 2014; Aznar et al., 2015; Arora and Verma, 2017). Siderophore production is one of the key PGP functions of bacteria, including rhizobia (Verma et al., 2011). Apart from mobilizing iron uptake by plants, siderophores produced by rhizobia increase nodulation and N fixation, as well as improve the adaptation of plants to disease-causing pathogens and stress (Jaiswal et al., 2021). Different studies have revealed the higher abilities of soybean nodulating rhizobia in the production of siderophores. Igiehon et al. (2019) demonstrated the higher levels of siderophore production by different species of soybean nodulating rhizobia, including *Rhizobium sp*., *R. tropici*, *R. cellulosilyticum*, *R. taibaishanense*, and *E. meliloti*. Similarly, Khandelwal et al. (2002) observed the production of siderophores by *B. japonicum* and improved nodulation in soybean under a sick-pot experiment. Regarding the ability of soybean nodulating rhizobia in siderophore production, it is worth exploring them by isolating them from diverse ecologies to obtain the most effective species that can produce siderophores for effective nodulation and N_2 fixation in soybean.

Indole-3-Acetic Acid (IAA) Production

Indole-3-acetic acid (IAA) is a naturally occurring auxin hormone with broad physiological effects. The hormone is produced through different pathways, which are indole-3-acetamide (IAM), indole-3-pyruvate (IPyA), tryptamine, and indole-3-acetonitrile (Lambrecht et al., 2000). It is well-documented that IAA is responsible for vascular tissues differentiation, elongation growth, apical dominance, lateral root initiation, fruit setting, and ripening (Dilfuza, 2011), whereas exogenous application of IAA from rhizobia promotes nodulation, root growth, and plant development in leguminous plants (Jaiswal et al., 2021). Several studies have identified different soybean nodulating rhizobia, which produces IAA associated with the promotion of nodulation and increased N fixation. Appunu et al. (2009) conducted an *in vitro* test of the IAA production of soybean nodulating rhizobia and observed that the species of rhizobia from the *Ensifer* group and *B. elkanii* demonstrated the good capability of producing IAA. Fukuhara et al. (1994) revealed that the exogenous application of *B. elkanii*, which produces IAA, increased the number of nodules in soybean. Similarly, Shi et al. (2002) investigated the production of IAA by soybean nodulating rhizobia. The species demonstrated different capabilities in synthesizing IAA such that the reference strains *B. japonicum* SEMIA 566 and SEMIA 5080 produced 1.00–15.55 μM, which was rated as low. Among the test isolates, 23 produced 16.6–50.0 μM rated as medium, while the other 8 isolates, together with *B. elkanii* SEMIA 587 and SEMIA 5019, and *S. fredii* USDA 205 and CCBAU 114, high concentrations (50–130 μM of reference strains. Depending on the reviewed studies, it is worth conducting more studies to obtain the rhizobia strains, which are highly effective in the production of IAA solely or together with N_2 fixation, and commercialize them as inoculum.

ROLE OF SOYBEAN-NODULATING RHIZOBIA IN THE SUPPRESSION OF SOYBEAN SOIL-BORNE PATHOGENS

Along with their ability to fix N, rhizobia also have a good ability to suppress soil-borne pathogens affecting plants (Farhat et al., 2017). Some species like *R. japonicum* (Al-Ani et al., 2012), *S. meliloti*, *B. japonicum*, and *R. leguminosarum* have been observed to suppress the common root-rot diseases caused by *Phytophthora clandestine*, *Pythium ultimum*, *Fusarium solani*, *Fusarium oxysporum*, *Pythium sp.,* and *Rhizoctonia bataticola* (Parveen et al., 2019). Soybean plants are among the legumes which are highly affected by soil-borne pathogens which cause root-rot diseases which limit the growth and yield of plants (Yang and Feng, 2001). *Macrophomina phaseolina* and *F. solani* are among the most important soybean root pathogens (Al-Ani et al., 2012). Some rhizobial species, including *Bradyrhizobium sp*, *S. meliloti,* and *Rhizobium sp*, have been observed to suppress *F. solani*, *Macrophomina phaseolina*, *F. oxysporum*, and *R. solani* in the rhizosphere of soybean. Some of the mechanisms reported include rhizobia producing antibiotics, hydrocyanic acid, and mycolytic enzymes, hence limiting the growth of soil pathogens (Das et al., 2017). These rhizobial species were observed to be effective in suppressing *F. solani*, *M. phaseolina*, *F. oxysporum*, and *R. solani* in the rhizosphere of soybean when applied in combination with mustard oil cakes and *Trichoderma harzianum* (Parveen et al., 2019). *Trichoderma harzianum* has been observed to be effective in the biocontrol of root rot pathogens (Afzal et al., 2013). Mustard oil cake is used as organic nitrogenous fertilizer with a high content of N, P, and K (NPK), increasing

uptake of N by plants as well as protecting plants from infection by nematodes, soil insects, and parasites (Parveen et al., 2019). Therefore, it is important to explore the new rhizobia species, which are capable and effective in suppressing the root rot nematodes and fungal pathogens causing the losses in the yield of soybean. It is also worth testing the multiple roles of rhizobia in fixing N, solubilizing P, suppressing root rot diseases, or preparing the inoculum with different species or co-inoculation of rhizobia with different roles and testing the compatibility effect. For instance, an inoculum containing different rhizobia species that fix N, solubilize P and suppress root rot disease causing-pathogens.

EFFECT OF SOYBEAN NODULATING RHIZOBIA IN PLANT GROWTH AND DEVELOPMENT

Soybean plants form symbiotic associations with rhizobia in the soil to form root nodules. The rhizobia fix atmospheric N_2, which is then used by the host plant. Apart from the symbiotic association, soybean roots can extract N from the soil or fertilizers (Simon et al., 2014; Takuji et al., 2017). The amount of N that is taken in the shoot of soybean plants is correlated with the yield of soybean seeds regardless of the N. The availability of N is very important for the improved and sustainable production of soybean. This can be achieved by investing in biofertilizers made from the rhizobia species, which are effective in fixing N. This is an affordable, environmentally friendly, and highly effective source of N in agricultural soils (Shi et al., 2002; Takuji et al., 2017; Reckling et al., 2021). Kassam (2019) reported that the potential of soybean to fix N is about 88-188 kg N/ha/year. When there is a low level of N in the soil, soybean can fix up to 300 kg of N/ha under inoculation with effective *Bradyrhizobiaum sp* (Ntambo et al., 2017). On the other hand, *Rhizobium spp* and *S. fredii* SMH12 are observed to increase soybean seed N up to 193 and 175 kg ha^{-1} under Oxisol soil with pH 5.4 as compared with non-inoculated treatment with a seed yield N of 168 kg ha^{-1} (Hungria et al., 2001).

The symbiotic performance of soybean nodulating rhizobia is assessed by evaluating the effect of nodulation on different plant growth parameters as well as the determination of plant N percentage in the shoot. For nodulation, the assessment is mainly on the number and dry weight of nodules per plant, while for plant growth parameters, the assessment is done on plant height, a number of leaves, root length, shoot and root dry weight, seed yield, N content in above-ground biomass and harvest index (Rodriguez-Navarro et al., 2011; Elkoca et al., 2015). Rodriguez-Navarro et al. (2011) conducted the field experiment on the inoculation of soybean with eight *S. fredii* strains against the standard inoculum of *B. japonicum* USDA110 (currently: *B. diazoefficiens* USDA110) strain, N-fertilized plants, and non-fertilized plants. An increase in the number of nodules per plant from zero in N fertilizer and none-inoculated soybean plants to a maximum of 106 for *B. japonicum* and 163 for *S. fredii* was observed. The dry weight of nodules per plant increased from 441 to 780 mg, the seed yield increased from 2,226 kg/ha in non-inoculated plants and 3,732 kg/ha in N-fertilized plants to an astonishing value of 4,041 and 4,338 kg/ha following *B. japonicum* and *S. fredii* inoculation, respectively. The seed N content of N-fertilized plants was 197 kg/ha, while in plants inoculated with *B. japonicum* and *S. fredii*, the seed N content was 252 and 230 kg/ha, respectively.

On the other hand, Chibeba et al. (2017) tested the symbiotic performance of indigenous *Bradyrhizobium sp* and *Rhizobium sp* in Mozambican soils and observed a significant relationship ($p < 0.05$) between the nodule numbers and their dry weight, nodule dry weight with shoot dry weight and total N of the shoot, as well as between shoot dry weight and total N. Similarly, Iturralde et al. (2019) reported a positive relationship ($p < 0.05$) between nodulation and plant growth parameters including shoot and dry weight per plant, above and below-ground biomass ratio, the N content of shoot and root, as well as ureides in the plant leaves. Similarly, Alam et al. (2015) observed a significant ($p \leq 0.05$) increase in soybean pod, stover, and seed yield in three of four soybean genotypes that were inoculated with *Rhizobium sp*. BARIRGm901 under field conditions. The results from the above studies imply that the soybean nodulating rhizobia strains which are effective in fixing N outperform the use of nitrogenous fertilizers for the attainment of an optimum yield of soybean. However, the performance of rhizobia is affected by many factors, including soil nutrients, soil reaction (acidity and alkalinity), and climate. These factors need careful consideration for the successful use of biofertilizers for the growth promotion function.

CONCLUDING REMARKS

Soybean-nodulating rhizobia are important parts of the ecosystem due to their symbiotic N_2-fixing activities with legumes. With the goal of bettering our understanding of this unique group of bacteria, the present review summarizes the approaches employed in characterization and studies of rhizobial diversity, symbiotic effectiveness, plant growth-promoting (PGP) functions, and suppression of soybean soil-borne pathogens. To obtain the most effective rhizobia species for a given application, extensive morphological, biochemical, and molecular characterization is required. Differentiating the rhizobia for further investigation requires morphological characterization, including colony characteristics and the gram reaction, as well as many biochemical studies. Essential biochemical assays such as antibiotic resistance are done to measure the survival and competitiveness of rhizobia in the soil. Carbohydrates utilization assays are undertaken to determine the potential of rhizobia to utilize different sources of carbon as their only source of energy because carbon is a crucial substrate for microbial activities, including rhizobia. Production of nitrogenase enzyme by rhizobia is tested to evaluate the capability of rhizobia in fixing N. Solubilization of essential nutrients such as P, K, and Zn as well as production of siderophores and IAA are tested as markers of PGP activities. Apart from these PGP functions, rhizobia's capacity to suppress pathogens that cause root rot disease is being explored as a

biological control agent. Genetic identification and taxonomic classification of the discovered organism are the primary goals of molecular characterization. Furthermore, molecular approaches are used to investigate gene activities such as symbiotic genes like *nodC* and *nifH*. It is apparent that although the inoculation of soybean with rhizobia can improve N_2 fixation, nutrients solubilization, and promote plant growth, these tend to differ with the type of rhizobia species. Despite notable research efforts into the ability of soybean nodulating in the suppression of soil-borne pathogens, there is still limited information about the availability of commercial rhizobia inoculum that suppresses root rot disease in soybean. Therefore, a complete understanding of the ecology of indigenous soybean-nodulating rhizobia concerning their genetic diversity and the environmental factors associated with their effectiveness is required. Such information can ultimately result in comprehensive knowledge about these soybean symbionts and increase their large-scale application for soybean inoculation and sustainability of agricultural systems.

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MDN, PAN, and PBV: conceptualization and methodology. MDN: original draft preparation. PAN and PBV: review and editing. All authors have read and agreed to the published version of the manuscript.

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