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Case Report

The role of Rhizobia toward food production, food and soil security through microbial agro-input utilization in developing countries

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ABSTRACT

Agricultural inputs such as fertilizers are becoming increasingly expensive and less available in developing countries, leading to decreased land productivity and food availability. Similarly, over-dependence on inorganic fertilizers and pesticides not only increases production costs but also poses a threat to the environment. Hence, alternatives to traditional agricultural inputs are necessary to achieve sustainable land productivity while maintaining environmental quality. Nitrogen (N)-fixing bacteria (rhizobia) are a group of plant growth-promoting bacteria that live in symbiosis with legumes. Their interaction with legume roots results in nodules that provide plants with additional nutrients through N-fixation, making legumes ideal crops due to reduced N fertilizer requirements. Despite their potential to improve land productivity and increase food production and security, the use of rhizobia is limited in developing countries due to limited research and agricultural microbial product production. Therefore, additional efforts are needed to increase the utilization of soil microbes to ensure food and soil security. The present review expounds on the role of rhizobia toward food production, food and soil security through microbial agro-input utilization in developing countries. Included in the review are the diversity of root-nodulating rhizobia, morphology and formation of legume, the role of nodulating bacteria for increased food production in developing countries, the application of nodulating bacterial technologies in food production in developing countries, and the implication of nodulating bacteria toward agricultural sustainability in developing countries. The review established that rhizobia are less utilized in developing countries as an option to increase food production and soil security due to limited research and agricultural microbial agro-input product production. Thus, additional efforts are required to increase soil microbes utilization to increase food production and ensure food security.

1. Introduction

The amount of agricultural land available for crop production is decreasing globally due to urbanization and industrialization, putting pressure on the limited available land [1]. This reduction of agricultural land has led to soil fertility decline and erosion from continuous cropping, resulting in the need for high use of agrochemicals like fertilizer, herbicides, and pesticides to maintain high productivity. However, these agrochemicals are not easily accessible in developing countries and are becoming more expensive worldwide. To address this issue, scientists are exploring ways to increase crop yields, such as breeding crops with higher nutrient efficiency, using transgenic crops that are resistant to pests and diseases, using wastewater with high nutrient levels in farming, and incorporating legume plants. Modern biotechnology has also been utilized in recent years to improve crop productivity by manipulating organisms, populations, and genetic components [2,3].

Despite several attempts to increase crop production in developing countries, different practices have not been sustainable for average farmers, especially smallholder farmers, since they come with higher economic, ecological, and environmental price tags. In this regard, developing countries may not be able to feed their growing population, which is currently around 7 billion and expected to reach 10 billion in 50 years, when Sub-Saharan Africa (SSA) will have approximately 2.12 billion people (UNDP, 2015). Thus, growing sufficient food in these

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countries will require various sustainable but environmentally friendly strategies and approaches. Therefore, it is necessary to assess ways of increasing agricultural productivity in developing countries using alternative mechanisms such as the use of plant growth-promoting bacteria (PGPR).

The PGPR, or Plant Growth Promoting Rhizobacteria, are a group of bacteria that play a vital role in the growth and protection of plants. These bacteria directly contribute to the growth of plants by providing essential nutrients and promoting root development. At the same time, they protect the plants from various abiotic and biotic stress factors, such as extreme temperatures, drought, and pests. Over the past few decades, scientists have made significant strides in understanding the functions of PGPR and other soil microbes in promoting plant growth. Despite this progress, the use of PGPR and other beneficial soil microbes is still limited in developing countries [4].

As the world faces the consequences of environmental damage and population growth, it is becoming increasingly important to find sustainable solutions for promoting plant growth. The use of PGPR and other environmentally friendly options is a crucial step in this direction. PGPR can help increase crop yields while reducing the need for harmful agrochemicals, making them a valuable tool in promoting sustainable agriculture. Owing to these benefits, it is increasingly becoming important to explore the full potential of PGPR and other environmentally friendly options for promoting plant growth.

Nitrogen-fixing bacteria, also known as rhizobia, play a crucial role in the growth and development of legume plants. These bacteria form nodules in the roots of legumes, where they fix nitrogen from the atmosphere and provide the plants with essential nutrients. The relationship between legumes and rhizobia is complex and involves the exchange of signalling molecules and other compounds [5]. Despite the important role of rhizobia in legume growth and food security, their use in developing countries is still limited. In Sub-Saharan Africa, for example, the application of rhizobia to increase food production is poorly understood and underutilized. There is a significant knowledge gap in this area, which limits the commercialization of rhizobia and potential to increase food production in these countries. The development of effective management strategies and an increased understanding of the role of rhizobia in food security is essential to enhance food production in developing countries. This systematic review of soil microbes toward food security, especially the nodulating root bacteria for increased food production in developing countries aims to identify the potential and application of legume-nodulating bacteria (LNB) towards food security, critical knowledge gaps, and recommendations for sustainable food production in the context of the United Nations Sustainable Development Goals (SDGs) such as Zero Hunger, Life on Land and Life Below Water. This information can help facilitate increased application and use of LNB for increased food production in developing countries and pave the way for the development of sustainable global food production systems.

2. Review methods

This systematic review aims to assess the potential and application of LNB in increasing food production and promoting food security in developing countries, with a focus on African and Southeast Asian countries. The review was conducted by searching peer-reviewed publications on the Web of Science, Research Gate, and Google Scholar, university dissertation repositories, government reports, and other sources for information on bacterial nodulation, legume nodule morphology and diversity, food production challenges, and the application of LNB technologies towards food production. The search query was narrowed down to precise key terminologies and words regarding LNB towards food security and biodiversity sustainability. In terms of spatial-temporal scope, this review covers the broad region of developing countries on the role of root nodulating bacteria for increased food production in developing countries, predominantly African and Southeast Asia countries that have been badly affected by climate change and disadvantaged in terms of technological advancement in food production. Although food production includes plant-based and animal-based food materials; in this review, only plant-based food production is considered because it is a primary, sustainable, and independent food production method. The review covers the period from the 1980s to the present and considers plant-based food production only. The findings of this review can help promote the increased use of LNB in developing countries for sustainable food production in line with the United Nations Sustainable Development Goals.

3. Diversity of root-nodulating rhizobia

Bacteria of the Rhizobiales order establish symbiotic relationships with leguminous plants to produce N-fixing root nodules. The symbiosis is determined by specific recognition signals molecules from the bacterial and legume partners plant. Rhizobia have the unique capacity to induce root nodules formation in the host plant by producing specific signal molecules called Nod factors [6–8]. The rhizobia also invade plant tissues resulting to differentiated root nodule. This differentiated form of the bacteria fix gaseous N (N_2) into ammonia (NH_3), which are later supplied to the host plant [7–10].

The rhizobial species are genetically diverse, mainly belonging to four families: Rhizobiaceae, Phyllobacteriaceae, Hyphomicrobiaceae, and Bradyrhizobiaceae. Within these four families, only a few genera (*Rhizobium, Azorhizobium, Sinorhizobium, Allorhizobium, Mesorhizobium,* and *Bradyrhizobium*) are capable of fetching N from the atmosphere to agricultural soils via legumes plants. Pawlowski [11] determined more than 300 isolates of legume bacteria alongside the Rhizobiales which constituted only 13% of the total isolates. Among the isolates, Bacillales (particularly *Bacillus*) were the dominant isolates from all host legumes and all elevations (63.5%), followed by Pseudomonadales (11.7%). Less than 3% of the isolates belonged to "Burkholderiales, Paenibacillales, Enterobacteriales, Actinomycetales, Sphingomonadales, Xanthomonadales, Chitinophagales, Brevibacillales, Staphylococcales, or Mycobacteriales". A few elevation-specific patterns emerged within the Bacillales and Pseudomonadales. Most bacteria associated with root nodules of legumes are widely distributed in distinct ecological zones within a single geographic region, but climate and host interactions may influence their distributions [12].

Despite this genetic diversity of rhizobia, it has become clear that these bacterial genera have many common genetic and biochemical characteristics related to their capacity to establish a successful symbiosis. These common factors include the capability to recognize specific signal molecules, such as flavonoids from the host plants [13], and to produce unique signal molecules such as the *Nod* factors which are not made by other related genera. Rhizobia can perform its functions in different areas because have specialized structural adaptations and regulations, which can work in growth conditions, presence of many toxic compounds (e.g., phenolics and enzymes), and capable of avoiding plant defence mechanisms. In this regard, a wide variety of cell surface characteristics of rhizobia are different from those of other related soil bacteria [14]. However, the identification of common adaptations is hampered by the fact that different plant-host species offer different habitats for the guest bacteria (leading to host specificity) [15,16]. Various bacterial traits have evolved convergently from many different genetic backgrounds. Recent studies have found rhizobia in indigenous and invasive legumes belonging to Papilionoideae and Mimosoideae subfamilies in South Africa, Tanzania, South America, and Southeast China [17]. These rhizobia are phylogenetically and taxonomically different from the traditional 'alpha rhizobia' and are termed 'β-rhizobia' as they belong to the β-subclass of Proteobacteria. There are also new reports of novel species of root-nodulating bacteria from the α-Proteobacteria, not known for several decades since discovering rhizobia [18,19]. This provides some insights into the status of the legume-*Rhizobium* host specificity concept and the loss of this specificity in several symbiotic associations that put the long-held dogma of host specificity of the legume-*Rhizobium* symbiosis in a dilemma [18,20,21].

4. Morphology and formation of legume root nodules

The root nodule is the result of a symbiotic relationship between legumes and rhizobia. The formation of the nodule is regulated by chemical signals exchanged between the plant and the bacterium. The bacterium initiates the root nodule formation process after receiving a signal from the host plant, which is usually in the form of flavonoids and their glycosides and biosynthetic precursors, chalcones. Once the bacterium receives the signal, it triggers the expression of the genes necessary for nodulation. The nodulation gene inducers vary in structure and their plant of origin [11]. The exchange of various nutrients takes place between the rhizobia and the host plant, including organic carbon, which is fixed by the plant and transported to the microbe, and N, which is fixed by the bacteroid and transported to the plant tissue in the form of ammonia and amino acids. The root nodule is a critical symbiotic relationship between leguminous plants and rhizobia bacteria. The process of nodulation is regulated by a series of chemical signals exchanged between the plant and bacteria. The bacterium initiates the root nodule formation after receiving a signal from the host plant, mainly through flavonoids and their glycosides, as well as chalcones, the biosynthetic precursors of flavonoids.

The first step of nodule formation begins when the nodulating bacterium receives a signal from the host plant. These signal molecules trigger the expression of specific bacterial genes required for nodulation. The nodulation gene inducers are classified based on their skeletal structure and plant of origin. Once the nodulation process has begun, rhizobia and host plants exchange various nutrients, including organic carbon. This carbon is fixed by the plant and transported to the bacterium, and N, which is fixed by the bacterium, and transported to the plant tissues in the form of ammonia and amino acids. The bacterium's capacity to fix atmospheric N_2 into a useable form is a critical component of the symbiotic relationship between the plant and bacteria. Nodulation not only provides the plant with a source of fixed N but also confers multiple benefits to the plant, such as increased resistance to environmental stress, improved soil health, and increased nutrient uptake. Additionally, the root nodules play an essential role in sustaining soil fertility and plant productivity, which is crucial for achieving food security in developing countries, where smallholder farmers face numerous challenges, including declining soil fertility, reduced crop productivity, and high production costs [11].

The root nodule symbiosis between leguminous plants and rhizobia is a complex process that is regulated by a series of chemical signals exchanged between the plant and bacteria. The nodulation process provides the plant with a source of fixed N, and its benefits to the plant are numerous, including increased plant productivity, improved soil health, and increased resistance to environmental stress. These benefits are crucial for achieving food security in developing countries, where smallholder farmers face numerous challenges.

5. Mechanisms of rhizobia in improving soil health and crop production in developing countries

The LNB are essential in increasing agriculture production through different mechanisms currently being commercialized to increase crop productivity in degraded and marginalized land (Gopalakrishnan et al., 2015).

The vital mechanisms that LNB or rhizobacteria (directly or indirectly) use to promote crop growth and productivity include the production of phytohormones, siderophore, phosphate solubilization (Fig. 1), and reduction of ethylene production (Herman, 2000). Several studies and researchers [22–25] have identified different bacterial isolates that can directly control plant physiology by mimicking the synthesis of phytohormones, which improves the availability of N and other plant nutrients in agricultural soils, thus accelerating crop growth and development. The different applications of LNB are further discussed in subsections 5.1 to 5.5.

5.1. *Phosphate solubilization in agricultural soils*

Phosphorus (P) is a macronutrient essential for plant growth and advancement, aiding in photosynthesis, energy, and sugar production and improving legume N fixation [13,21,26,27]. In tropical agricultural soils, it is estimated that only 0.1% of total P is available and accessible for plant uptake, and 99.9% is available in an insoluble form, making it unavailable for plant uptake [28,29]. Rock phosphate is the sole economic basis of P but its accessibility is limited and skewed. Generally, the precipitated P form in the soil (mono- or orthophosphate) is adsorbed by aluminium or iron oxides via ligand exchange, further limiting its availability. Therefore, mobilizing inaccessible P to plant-available P is thus necessary to prolong crop yields [30,31].

Phosphate-solubilizing microorganisms significantly transform the

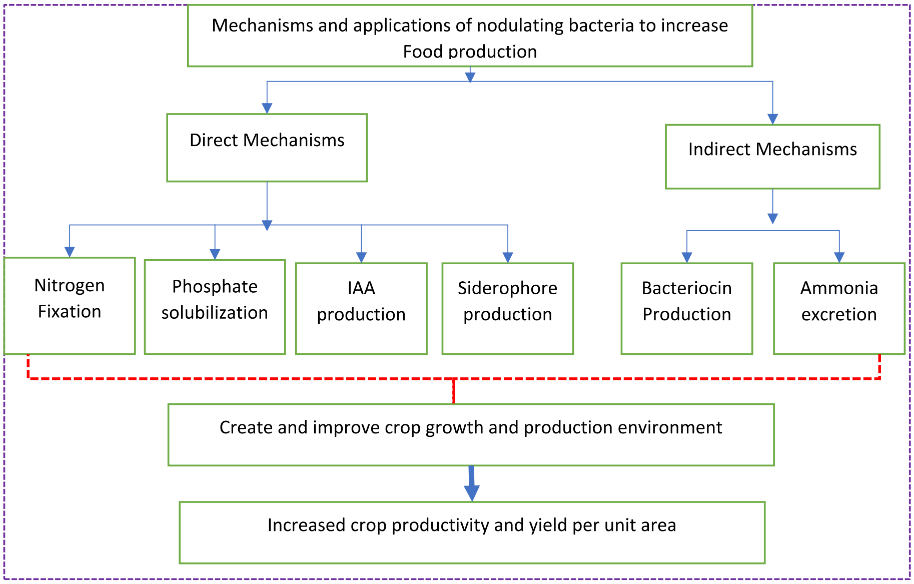

Fig. 1. A schematic illustration of how LNB directly or indirectly helps to achieve increased food production in developing countries.

unavailable form of P into the available form by lowering the soil pH through organic acids, which further mineralize organic P with acid and alkaline phosphatases. Bacteria solubilizing phosphate, such as rhizobacteria, can reduce the activity of P fertilizer by up to 50% while maintaining high crop yields. Common LNB species such as *Rhizobium, Mesorhizobium, Bradyrhizobium*, and other non-specified LNB can solubilize P from its insoluble sources and make it available for plant uptakes. For example, the study by Janati et al. [32] determined that among 20 *Sesbania grandifora* rhizobia, about 80% of the isolates (18 isolates) were capable of significantly solubilizing phosphate, and their solubilization index was observed to range from 1.96 to 4.85, thus ensuring increased P for crop uptake and consequently high crop yield for food security in developing countries.

5.2. Indole acetic acid production

Indole acetic acid (IAA) is a plant growth hormone considered the most important representative of auxins. Some common precursors for natural biosynthetic pathways are tryptophan and derivatives of indole. The IAA is a regulator of several biological processes such as cell division, seed germination, cell elongation and differentiation, root hair development, and fruit development, thus vital in crop growth and development. Parallel to plants, IAA also affects the survivability of bacteria and their resistance to plant defense. Microbes isolated from the rhizospheres of different crops have the capability of IAA production as secondary metabolites due to the rich supply of substrates. For instance, Sridevi and Mallaiah [33] established that about 80% of rhizospheric microbes possess the capability of synthesizing and liberating auxins as secondary metabolites. Sridevi and Mallaiah [33] found 26 IAA-producing *Rhizobium* strains from root nodules of *Sesbania sesban* (L.) from different locations in Andhra Pradesh, India. However, only five strains could produce the maximum IAA in yeast extract mannitol medium supplemented with L-tryptophan. A study by Etesami et al. [34] also reported enhanced shoot biomass and root length after inoculation of seedlings (host plant) with IAA-producing isolates. In addition, IAA-producing bacteria enhanced vegetative plant growth. However, their utilization in most developing countries is limited primarily due to inadequate access to biotechnological laboratories, but utilization of IAA-producing isolates can significantly improve land productivity and ensure food security.

5.3. Siderophore production

Since iron is one of the requisite microelements for all living cells, its availability is limited. The dominant form of iron in the soil is present as ferric iron (Fe^{3+}), with very low solubility. Microorganisms have established the strategies of acquiring and assimilating iron by secreting iron chelators called siderophores. Siderophores chelate iron and alter it to a soluble form, and they are commonly produced by aerobic, facultatively anaerobic bacteria and fungi under iron-limiting conditions. Sridevi and Mallaiah [33] studied 26 *Rhizobium* strains isolated from root nodules of *Sesbania sesban* (L.) for their ability to produce siderophores. It was found that nine strains could synthesize catechol-type of siderophores in culture after 4 hours of incubation at a neutral pH.

To date, nearly 500 siderophores are reported from selected microorganisms. Siderophores are generally classified as hydroxamates, catecholate, salicylates, carboxylates, and new polycarboxylates. Studies show that agricultural soils also contain siderophore-producing bacteria, which mainly belong to the rhizobium BICC 651, and are observed to perform better at soil pH of 6.5 and 30 °C [35,36]. This indicates that isolates for siderophore-producing bacteria can be isolated from agricultural soils to get isolates that are well adapted to the environment for better results. The production of siderophores by *Rhizobium* increases plants' chance to utilize Fe from agricultural soils, thus ensuring better plant growth and increased crop yields; however, their commercial utilization is limited in developing countries.

5.4. Ammonia excretion

Ammonia production by rhizobia plays a vital role in biocontrol activity, indirectly influencing plant growth. *Rhizobium* spp fixes atmospheric N_2 in symbiotic association with a leguminous plant. The main procedure, converting atmospheric N to ammonia, takes place inside the nodule by the Bacteroides via the nitrogenase enzyme complex, which tends to be irreversibly sensitive and damaged by oxygen. However, the ammonia formed in the Bacteroides is assimilated by plant enzymes in the plant cytosol. Several processes exist utilizing which ammonia can be produced, viz., nitrite ammonification, degradation, and decarboxylation of amino acids to create biogenic amines with ammonia, deamination, and the urease-mediated hydrolytic degradation of urea [37,38]. This form of ammonia cannot be utilized by plants but may be available through the biological N-fixation (BNF) process, developed only in prokaryotic cells. Inoculation with such bacteria enhances plant growth by converting atmospheric N to ammonia, making it an available nutrient for plant growth. The ammonia production by LNB varies among species where *Pseudomonas* (which tends to intensify nodulations) [37,38] has higher ammonia production (94.2%) than *Rhizobium* (74.2%) and *Azotobacter* (45.0%) [39]. To remain within this review's scope, readers interested in the mechanism for rhizobacteria promoting crop growth are advised to read [13,40].

5.5. Nitrogen fixation as an alternative to inorganic nitrogenous fertilizers

Nitrogen is a critical nutrient for all living organisms and is crucial for plant growth and development [41]. The atmosphere contains a vast amount of nitrogen, but it is not available in a form that can be used by plants. Therefore, plants rely on bacteria and fungi to convert atmospheric nitrogen into useable forms such as nitrates (NO_3) and nitrites (NO_2), which are essential for plant growth and health. This process is called Biological Nitrogen Fixation (BNF) (Fig. 2). The microorganisms capable of converting atmospheric nitrogen into a useable form for plants are called N-fixing bacteria, of which the most well-known is Rhizobium. This process is widely used in modern agriculture to reduce the use of synthetic nitrogen fertilizers and create more sustainable and profitable farming while preserving ecosystem quality. By using N-fixing bacteria, farmers can reduce their dependence on chemical fertilizers, which can be costly and have negative environmental impacts [42].

The increasing interest in using rhizobia as biofertilizers in smallholder agricultural systems in sub-Saharan Africa has led to the identification of many tropical rhizobia strains and the development of inoculants containing diverse strains for use as biofertilizers. However, despite the promise of this technology, it has not received much attention in Africa and remains largely unexplored due to various constraints. Nevertheless, a few biofertilizers have been developed in developing countries, particularly in South Africa, due to limited resources and technological capabilities for isolating and concentrating specific bacterial species.

In recent years, there has been a growing interest in utilizing N-fixing microbes as a means of biofertilization as an alternative to the use of chemical mineral fertilizers in agriculture. Chemical mineral fertilizers are commonly used in conventional agriculture, but their use has been linked to negative environmental impacts, making it crucial to explore alternative methods. This has led to several studies and efforts aimed at promoting the use of N-fixing microbes as a biofertilizer. The goal is to provide a more sustainable and environmentally-friendly solution to help farmers increase soil fertility and crop yield while reducing the need for chemical mineral fertilizers. By utilizing these N-fixing microbes, farmers can help maintain the health of their soil and crops, while also contributing to the conservation of the ecosystem.

Nitrogen-fixing microbes use nitrogenase enzymes and mechanisms to fix N (Gouda et al., 2018). These bacteria convert tons of N to ammonium (NH_4^+), nitrite (NO_2^-), and nitrates (NO_3^{2-}) and add it to the soil, allowing plants to survive even in nutrient-poor soils. These

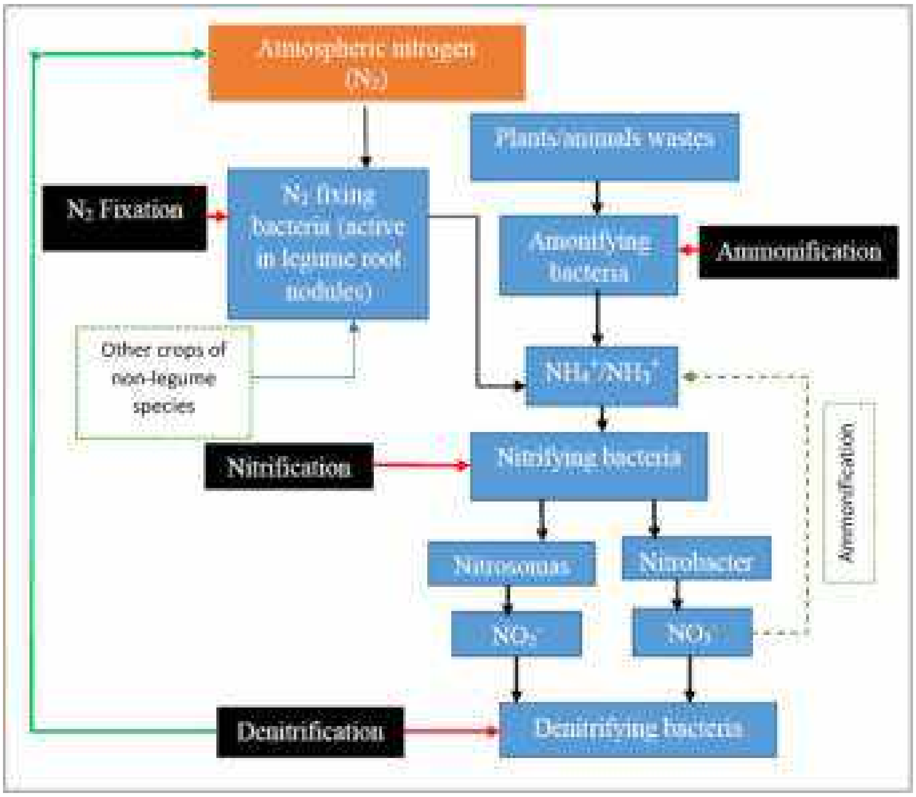

Fig. 2. The schematic representation of the N cycle shows four roles of bacteria as indicated by red arrows in the cycle (adapted from Ojija et al. [43]). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

bacteria are divided into free-living bacteria (non–symbiotic) and symbiotic (mutualistic) bacteria. The free-living bacteria include *Cyanobacteria* (blue-green algae), *Azotobacter, Azolla, Azospirillum, Agrobacterium*, *Clostridium*, *Gluconobacter, Flavobacterium,* and *Herbaspirillum*. They are habitually associated with non–legumes [44]. *Azospirillum* species and *Frankia* are associated with cereal grasses and certain dicotyledonous species (actinorhizal plants). *Rhizobium* and *Bradyrhizobium* are associated with leguminous plants (Fabaceae) or members of the pea family. The symbiotic N-fixing bacteria live in the root hairs of the host plants. Nitrogen-fixing bacteria are also amonifying, nitrifying, and denitrifying bacteria (Fig. 2). Amonifying bacteria release ammonia from organic compounds, i.e., dead plants and animals. This process is known as ammonification and is important to ensure the release of NH_4–N from organic materials to be available for other N cycle chemical reactions or plant uptakes for increased crop and food production; however, very few plant species can utilize direct NH_4–N for its biological processes.

6. Application of nodulating bacterial technologies for increased food production in developing countries

The increasing interest in using rhizobia as biofertilizers in smallholder agricultural farming systems of Sub-Saharan Africa (SSA) has led to the identification of many tropical rhizobia strains and the study of their diversity. To enhance soil fertility and promote symbiotic N fixation in legumes, inoculants containing a variety of rhizobia strains have been developed and used as biofertilizers. Worldwide research on plant-rhizobacterial interactions has led to the formulation and commercialization of rhizobacterial biofertilizers, providing a promising technology for sustainable soil and crop health [45]. Despite its potential, the use of rhizobacterial biofertilizers remains largely unexplored in Africa due to various constraints such as limited resources and laboratory facilities for isolating and concentrating specific bacterial species. Despite these challenges, a few biofertilizers have been developed in developing countries, particularly in South Africa, as shown in Table 1 due to limited resources and lab facilities and technology for isolations and concentration of a particular bacterial species.

Due to the growing population in developing countries, the amount of arable land has decreased over the years [46]. As a result, traditional practices such as shifting cultivation and fallowing, which were used to improve soil fertility, are no longer feasible [47]. This has led to a decline in soil fertility and land productivity in tropical countries. Many smallholder farmers in these countries cannot afford or have access to agrochemicals, but their improper use is causing environmental

Table 1
Some of the commercially developed and available Rhizo-biofertilizer in sub-Saharan Africa.

Rhizobacteria	Product name	Company	Origin/ Country
Rhizobium	SeedQuestR	Soygro Ltd	South Africa
Azospirillum brasilense	Mazospirflo, Azo-N	Soygro Ltd	South Africa
Bacillus sp	Lifeforce, biostart, waterbac, FirstBase	Microbial Solution Ltd	South Africa
Bacillus sp., *Enterobacter* spp., *Pseudomonas*, *Rhizobium*	Organo	Microbial solution Ltd	South Africa
B. subtilis	B-RUS, Extrasol	Ag-Chem Africa Ltd	South Africa
Bradyrhizobium elkanii	Likuiq Semia	Microbial Solution Ltd	South Africa
Bradyrhizobium	Nodumax	IITAb	Nigeria
Not revealed	Biofx	MEA Fertilizer Ltd	Kenya
Bradyrhizobium japonicum	Soyfo, Vault N	Soy Soygro Ltd	South Africa

Adapted with modification from Aloo et al. [45].

degradation and contamination [48,49]. Additionally, the cost of fertilizer has doubled in 2021 compared to the prices from 2005 to 2019, and this has resulted in decreased crop productivity and lower yields for smallholder farmers, putting food security at risk. Therefore, the availability of cheap and sustainable methods to supplement plant nutrients as an alternative to commercial fertilizers is crucial for food security and achieving the United Nations Sustainable Development Goal of Zero Hunger.

Nitrogen is the primary macronutrient required by plants for their growth and biochemical processes, thus contributing significantly to crop growth and yield. However, the inability of plants to utilize the freely available atmospheric N (N_2) makes N the most limiting nutrient in agricultural fields. Only bacteria and archaea can utilize free N_2 from the air by converting it into NH_3, which is one of the two plant-utilizable N forms. Since legumes can engage in symbiotic N-fixation, where they establish a mutualistic relationship with N-fixing bacteria, they can easily waive the necessity for artificial N fertilizers. Although chemical fertilizers are used in small and large commercial farming worldwide to satisfy the food and feed requirement of the world, their usage in developing countries is still low compared to the demand of 4302 tons per year [50]. Besides, these chemicals are linked to the declining diversity of important soil microbes in agricultural soils which present huge threats to the sustainability of global food production systems [51].

A diagrammatical illustration of how nodulating bacteria may directly or indirectly influence land productivity and food security in developing countries is shown in Fig. 3.

Although LNB are constantly being researched and commercialized as biofertilizers in the world to increase food production, their roles in food security are not well characterized and documented in the developing countries of Africa and Southeast Asia. A summary of some reviews on the use of LNB for improved food and soil security in developing countries is provided in Table 2. Nodulating bacteria, or biofertilizers, are plant-specific and capable of converting free N gas from the atmosphere to useable form by plants through root nodules of legume plants. The accumulated N helps to accumulate N-rich biomass, which is either used as food or used as green manure, helping in the conversion of futile land into fertile ones with improved soil fertility important parameter for increased land productivity and food security in developing countries (3). Nodulating bacteria are host-specific rhizobial strains that can be used as a potential alternative to nitrogenous fertilizers. They promote the host plant's growth and development and enhance its endurance under stress [52]. Even though rhizobia's performance depends on many factors, such as soil physicochemical properties, temperature, and vegetation, they have a tremendous capacity to fix N and adapt quickly in N-poor soils. Increasing the production of grain legumes is well recognized as a vital component of effective, sustainable strategies. Using legumes' capability to convert atmospheric N by symbiotic rhizobia presents the potential substitute for mineral N fertilizers and enhances crops' biological yield. The establishment of legume root nodules to provide a functioning N_2-fixing symbiosis requires ample root-nodulating bacteria in the soil or to be

Table 2
A summary of reviews on the use of LNB for improved food and soil security in developing countries.

Review title	Reference
Improving soil health and soil security for food and nutrition security in Nepal	Tripathi et al. [55]
The role of legume-*Rhizobium* symbiosis in sustainable Agriculture	Ohyama et al. [56]
Role of plant growth promoting rhizobia strains in agriculture for sustainable crop yield (A Review)	Ladan et al. [57]
History of Rhizobia inoculants use for improving performance of grain legumes based on experience from Nigeria	Abdullahi et al. [58]
Influence of rhizobium and virus inocula on growth and yields of Cowpea: A Mini-review	Oyatokun et al. [59]
Distribution, characterization and the commercialization of Elite Rhizobia Strains in Africa	Wekesa et al. [60]
The role of legumes in the sustainable intensification of African smallholder agriculture: Lessons learnt and challenges for the future	Vanlauwe et al. [61]
Potential of native rhizobial isolates to improve biological nitrogen fixation and growth of common bean and soybean in smallholder farming systems of Kenya	Jalloh et al. [62]
Competency of rhizobial inoculation in sustainable agricultural production and biocontrol of plant diseases	Kabede [63]
Microbial inoculants for soil quality and plant health	Alori et al. [64]
Meta-analysis of the effects of rhizobia inoculants and phosphorus fertilizer on soybean nodulation in Africa	Kanomanyanga et al. [65]

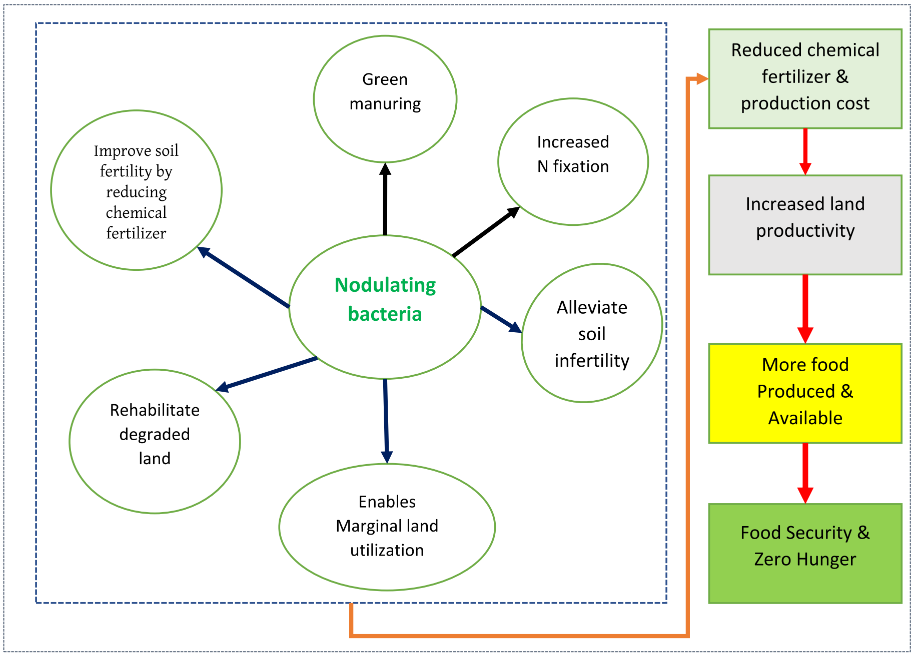

Fig. 3. A diagrammatical illustration of how nodulating bacteria may directly or indirectly influence land productivity and food security in developing countries (Source: Authors).

provided during sowing [53]. However, with the introduction of rhizobial strain establishment, the persistence and efficacy generally decrease with an increase in the population density, perhaps due to the possibility of negative microbial interaction or incompatibility with the other soil microbes within the rhizosphere. Therefore, native rhizobial strains can serve better as biofertilizers, improving soil biodiversity conservation [54].

Like other parts of the world, bio-fertilization limits the adverse effects of the excessive use of inorganic fertilizers on below-ground biodiversity in developing countries. Since rhizobia are poorly motile in soils, the point of delivery into the ground determines the nodulation pattern. Inoculation with compatible and appropriate rhizobia may be necessary, where a low population of native rhizobial strains predominates and this is one of the solutions the farmers can utilize for optimizing grain legume yields. Mondal et al. [66] recently showed that inoculation of abiotic stress-tolerant cluster bean rhizobial isolates enhanced 80–90% nodulation efficiency and plant growth over uninoculated control. In contrast, the study by Van Heerwaarden et al. [67] established the inoculation response of rhizobium to soybean across SSA, where the average yields were estimated to be about 1343 and 1227 with and without inoculation respectively. This shows that inoculation of legumes with nodulating rhizobacteria and biofertilizers can greatly enhance yields and food security in developing countries.

Furthermore, rhizobia are essential in reducing toxic trace metals to soil inhabitants and are known to reduce the availability of plant nutrients and limit crop productivity [47]. For example, the *Rhizobium* KG2 isolated by Li et al. [68] from soybean nodules was observed to reduce Cadmium (Cd) toxicity by 120 mg/L. In pot soil containing 50 and 100 mg/kg of Cd^{2+}, the *Rhizobium* strain reduced 45.9% and 35.3% of Cd in soybean roots respectively, and improved the root and shoot length, N content, biomass, and yield per unit area of the plants. Thus, applying LNB in agricultural soils can increase crop productivity and food safety by reducing the levels of toxic metals that accumulate in plant products, thus reducing the human health risks associated with heavy metals.

7. The implication of nodulating bacteria toward agricultural sustainability in developing countries

The role of soil microbes in humus formation is due to their ability to decompose organic matter. When the leaves or plants and animals die, microorganisms decompose them, allowing the humus to mix with the soil. Mineral weathering via chemicals and forces exerted by microbial communities thus contributes to soil formation, ensuring plant nutrient recycling and allowing sustainable agroecosystems' sustainable land productivity [69]. The exudates from bacteria and decomposed cells in soils are also responsible for enhancing the soil organic matter and improving the soil structure, function, and quality [70]. The inoculation of bacteria inocula and organic fertilizer can significantly improve soil fertility and aggregation and guarantee agricultural productivity and sustainability [71]. Furthermore, microbes such as fungi give tropical plant roots access to nutrients in the soil by forming close associations with tree roots. For example, most vascular tropical plants' roots and tiny root hairs are associated with mycorrhizal fungi whose hyphae provide an efficient absorptive structure. It is estimated that nearly 90% of all tree roots are in these associations. These symbiotic associations are called mycorrhizae, including those that live either on the plant surface (ectotrophic or sheathing) or in the host (endotrophic or vesicular–arbuscular). The mycorrhizal associations are involved in nutrients, e.g., N and P uptake, and transfer from the soil to the roots [23]. In addition to nutrient uptake, the hyphae secrete enzymes capable of breaking down organic molecules and making inorganic nutrients available to plants [72]. In addition, mycorrhizal associations support nutrient cycling, growth, and primary productivity in tropical rainforests and the plant community structure. It facilitates water uptake by the roots and enhances their resistance to pathogens, enabling tropical trees to exchange carbon through a fungal mat. Overall, this association is valuable to both parties; the plants gain nutrients, whereas the fungi obtain carbohydrates from the plant.

Furthermore, the microbes can potentially restore the fertility of degraded habitats and improve soil organic matter, remediate soil structure and stability, nutrient availability, and aggregation through various processes [41]. The fungal cells can release mucilaginous exudates composed of extracellular surface polysaccharides. These exudates are responsible for forming aggregates, which help improve soil aeration and porosity. Bacteria release exopolysaccharides that form organic–mineral complexes, which help bind soil particles into aggregates. Bacterial inocula can increase nutrient bioavailability through N fixation and P mobilization [23], potassium, and iron in crop plants. This inoculation is vital for restoring degraded soils. Compared to single inoculum, co-inoculation of bacteria and fungi are advantageous for restoring fertility and the organic matter content of the soil. For instance, N-fixing bacteria contribute 5–20% to the total N demand of grassland and savannah annually [70]. All these ensure increased land productivity and food production but also the sustainability of the agroecosystem. In general, the fundamental mechanisms through which bacteria and fungi promote soil aggregation and nutrient bioavailability include N fixation, P, K, and Fe mobilization through producing organic acids and siderophores, and improving land productivity and sustainability of the agro-ecosystem is highlighted in Fig. 4.

8. Contribution of rhizobia to soil security

Rhizobia and other soil bacteria can be used to enhance soil security in many ways. Rhizobia have the unusual ability to fix atmospheric nitrogen and transform it into a form that plants can use. Legumes and humans coexist in a symbiotic connection that reduces the need for synthetic nitrogen fertilizers. Farmers can improve soil fertility and cut back on the use of pricey chemical fertilizers by including legumes in crop rotation or intercropping systems. the unique ability of rhizobia to convert atmospheric nitrogen into a form (ammonia) that is readily available to plants, allows legumes and other crop plants to thrive without or with less need for synthetic nitrogen fertilizers [74]. Thus, the promotion of the use of rhizobia can significantly enhance soil fertility and reduce the dependence on the use of synthetic fertilizers which are usually highly-priced and not affordable to smallholder farmers [74,75].

Rhizobia are one of the important soil bacteria that contribute to the preservation of soil structure and fertility. By helping to create and maintain soil aggregates, they increase soil porosity, water infiltration, and nutrient retention. This improves the soil's general health and productivity and increases its resistance to erosion and deterioration [75]. The presence of rhizobia and other beneficial soil microbes contributes to the development of healthy soil structure which positively creates stable aggregates, thus improving soil porosity and increasing water infiltration and retention capacity. These factors enhance the soil's ability to hold water, reduce erosion, and improve water management, especially in areas that are prone to drought or water scarcity.

Suppression of disease: Some strains of rhizobia are reported to possess biocontrol properties, suppressing the growth of soil-borne pathogens and pests. Capable of suppressing plant infections and illnesses. Rhizobia and other advantageous microbes can engage in antagonistic interactions with undesirable ones, defending plants from illness and minimizing the need for chemical pesticides [74–76]. By reducing the negative effects of pesticide use on the environment, this method supports sustainable agriculture. This natural disease suppression reduces the need for chemical pesticides and promotes a more sustainable and environmentally friendly approach to pest management. Rhizobia improve the soil's built-in defensive mechanisms, promoting long-term soil health and crop protection.

Increased nutrient availability: In addition to fixing nitrogen, soil bacteria can mobilize and solubilize additional vital minerals for plants, including phosphorus, potassium, and micronutrients. Thus, rhizobia

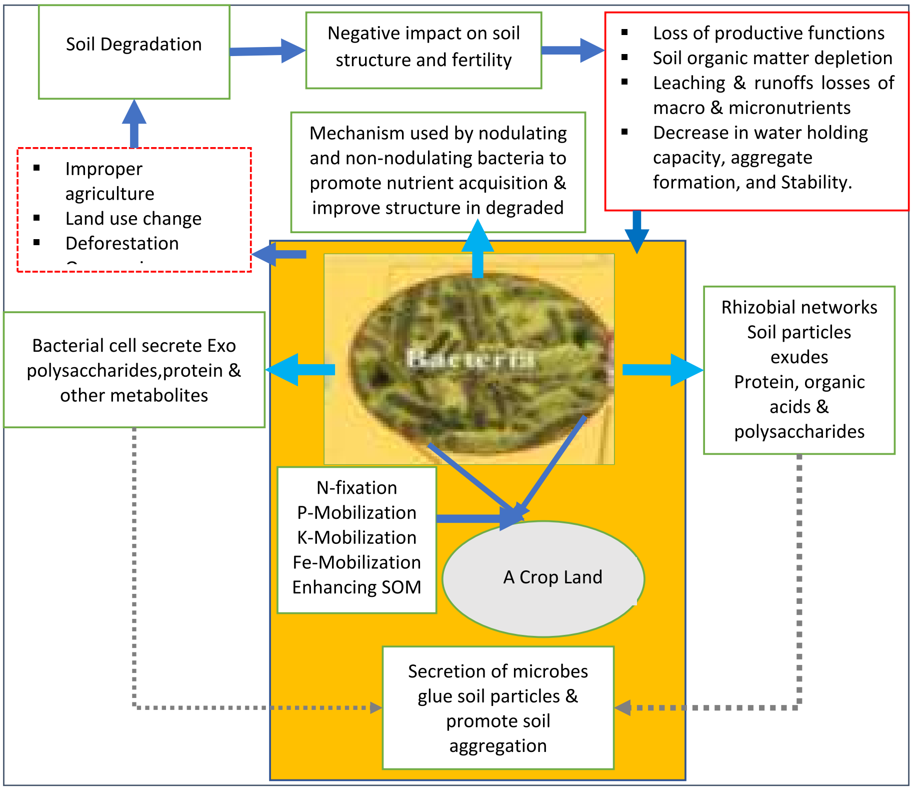

Fig. 4. The schematic shows the basic mechanisms bacteria use to improve soil organic matter, nutrient availability, and aggregation (Adapted with modification from Rashid et al., [70,73].

use in agriculture enhances the uptake and utilization of nutrients, resulting in healthier and more fruitful crops. The decomposition of organic matter is carried out by soil microbes, which promotes nutrient cycling and the release of nutrients that have been trapped in organic wastes. The organic matter content of the soil is increased by this process, which is important for soil fertility, water retention, and carbon sequestration. Farmers can lessen their reliance on pricey agricultural inputs, improve the health and fertility of the soil, and encourage sustainable land productivity by utilizing the potential of rhizobia and other soil bacteria. Long-term soil security can be achieved by putting practices in place that promote the utilization of advantageous soil bacteria, therefore, ensuring the availability of fertile and fruitful land for future food production.

Nutrient cycling: Rhizobia play a crucial role in nutrient cycling within the soil. Through their symbiotic relationship with legumes, they enhance the availability of essential nutrients, including nitrogen, phosphorus, and potassium, by breaking down organic matter and releasing these nutrients into the soil. This process improves soil health and nutrient retention, leading to enhanced productivity and reduced nutrient loss.

Biodiversity and ecosystem resilience: Within agricultural systems, the use of rhizobia and other soil bacteria fosters biodiversity. Rhizobia and legumes work in harmony to promote the growth of numerous plant species, which strengthens the ecosystem. Enhanced soil structure, nutrient cycling, and pest management are all benefits of increased biodiversity that eventually improve agricultural lands' overall sustainability and long-term productivity [74–76]. Rhizobia and other soil bacteria can be used as agricultural inputs to increase soil fertility, nutrient cycling, water retention, disease suppression, and overall ecosystem resilience, which can all lead to improved soil security. Thus, utilizing soil microbes offers a sustainable approach to agricultural production, ensuring long-term food security while maintaining the health and productivity of our soils. It does this by reducing the reliance on expensive and environmentally hazardous inputs, such as synthetic fertilizers and pesticides.

9. Conclusions and recommendations

The present review highlights the importance of LNB in promoting food production in developing countries, but much more needs to be done to realize its full potential. One of the key areas that need attention is making LNB more accessible to small-scale farmers to improve their crop yields. Despite its significance, the utilization of LNB for nutrient augmentation and recycling remains relatively unknown and understudied in most developing nations, largely due to the paucity of research and the limited availability of microbial agro-input products. This underscores the need for more initiatives to be launched to maximize the benefits of LNB in enhancing food production and security in these countries. Given the many challenges facing developing nations, including food insecurity and poverty, the need to explore innovative and sustainable agricultural solutions is more pressing than ever. With a large proportion of the world's population living in these countries, ensuring food security and stability is of the utmost importance. LNB represents a promising avenue for promoting sustainable agriculture and improving food production in these regions. By focusing on the development and dissemination of LNB products, smallholder farmers in developing nations could be empowered to enhance the productivity of their farms and improve their livelihoods. It is widely recognized that the use of chemical fertilizers, although critical for increasing food production, has significant negative impacts on the environment. The LNB represents a more sustainable and environmentally-friendly alternative, and its widespread adoption could help mitigate these impacts. Additionally, LNB has the potential to help address the issues of soil degradation and soil fertility decline, which are prevalent in many developing countries. The ability of these microbes to improve soil health and fertility, while simultaneously augmenting the nutrient availability to crops, is truly remarkable. However, to achieve these benefits, there is a need for more research to be conducted into the diversity, ecology, and applications of LNB in developing nations. There is also a need for more investment into the development of microbial agro-input products, which would make LNB more accessible and affordable for smallholder farmers. These efforts would go a long way in promoting sustainable agriculture, increasing food production and security, and ultimately improving the livelihoods of people in developing nations. While the significance of LNB in boosting food production in developing countries has been emphasized through this review, further work is necessary to realize its full potential. Specifically, there is a need to focus on making these microbes more accessible to small-scale farmers as a means of improving their crop productivity. However, the application of LNB for nutrient enhancement and recycling remains largely under-researched and not well-understood in most developing countries, due to the limited attention given to research and production of microbial agro-input products. Therefore, there is a pressing need for more efforts to be put in place to ensure that the full benefits of LNB can be leveraged to improve food production and security in these countries.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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