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Sinorhizobium and sustainable farming: Genomic approaches

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Abstract:
Global population growth requires highly efficient and environmentally sustainable agricultural technologies that can ensure food security with minimal environmental impact. As an alternative to chemical preparations, organic farming uses biological mechanisms to provide plants with nutrients. This review systematizes the current data on the genomics of nitrogen-fixing bacteria of the genus *Sinorhizobium*.

The review covered articles published in 1993–2025 and indexed in Scopus, MDPI, ScienceDirect, and Google Scholar. The metadata were processed in Zotero and VOSviewer.

The review summarizes information about the structure of *Sinorhizobium* genomes, key genes, and regulatory networks involved in the formation of symbiosis with host plants. It focuses on the molecular mechanisms that determine the effectiveness of biological nitrogen fixation and transport of iron, zinc, and phosphates. The obtained genomic data may be used to develop tailored biological products capable of increasing crop yield and stress resistance by targeted modification of the rhizosphere microbiome.

The latest scientific achievements and solutions demonstrate a great potential for sustainable agricultural technologies that replace chemical fertilizers with microbial communities. This approach reduces environmental risks and ensures a long-term productivity of agroecosystems, supporting climate resilience biodiversity conservation and stable agricultural development.

Keywords: Organic farming, *Sinorhizobium*, symbiotic nitrogen fixation, phosphorus solubilization, siderophores

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INTRODUCTION

Global population growth fuels the demand for food resources while intensifying human-induced pressure on agricultural systems [1, 2]. In this context, reliable food security requires larger crop yields. Mineral fertilizers increase crop production by providing plants with bioavailable nutrients. Therefore, enhancing their efficiency is a top propriety for agricultural science [3, 4].

Russia being a high-intensity agricultural country, mineral fertilizers remain fundamental for boosting crop yields. The most popular fertilizers contain such essential macronutrients as nitrogen, phosphorus, and potassium [5]. Nitrogen and phosphorus fertilizers are essential as these macroelements are limiting nutrients across most agricultural landscapes [6].

However, increasing fertilizer application rates does not necessarily lead to a proportional increase in crop yields and is often associated with significant environmental risks [7, 8]. Excessive and uncontrolled use of chemical nitrogen fertilizers contributes to soil degradation, nitrate contamination of aquatic ecosystems, and deterioration of air quality, ultimately posing significant risks to public health [9–12]. Phosphorus fertilizers cause similar environmental risks, particularly metal accumulation and ecosystem degradation [13, 14]. Addressing these issues requires a fundamental shift to sustainable agricultural practices that maintain high

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productivity while minimizing environmental impact and preserving ecosystems [15–18].

Organic farming systems represent the most effective approach to high-yield crop production. These systems use no synthetic pesticides, mineral fertilizers, or genetically modified organisms at all stages, from seed to harvest. Plant growth regulators and seed treatments are subject to strict regulations that exclude the application of synthetic chemicals [19, 20].

To improve soil fertility and plant resistance to adverse environmental conditions, organic farming utilizes environmentally friendly methods, e. g., organic fertilizers and microbial preparations [21]. Microbial fertilizers increase the diversity of soil microorganisms by bolstering beneficial bacterial and fungal communities [22]. These soil microorganisms improve plant resistance by changing the soil acidity, enhancing the organic carbon content, and displacing pathogenic microorganisms [19]. Furthermore, certain rhizospheric microorganisms can fix atmospheric nitrogen or mobilize phosphorus and potassium, thus providing plants with bioavailable nutrients [23, 24].

Present-day microbial preparations feature a wide range of beneficial microorganisms. The market offers preparations based on different categories of microorganisms: nitrogen-fixing bacteria (*Azotobacter*, *Azospirillum*, *Rhizobium*); phosphate-mobilizing microorganisms (*Pseudomonas*, *Bacillus*); phytopathogenic antagonist fungi (*Trichoderma*, *Gliocladium*, *Coniothyrium*); and plant growth-stimulating bacteria (*Bacillus*, *Pseudomonas*).

Despite the vast array of microbial products deployed for plant protection and growth promotion, their integration into intensive agricultural systems remains associated with several significant limitations. The key challenges include the high variability in efficacy across different agroclimatic and soil conditions, the logistical complexities, the high cost of the final product, and the lack of standardized guidelines for rational use. Moreover, microbial products often have to compete with traditional chemical crop protection methods [25, 26]. These limitations often come from a poor understanding of the genetic and molecular mechanisms that determine the functional properties of microorganisms used in biopreparations.

Genomic analysis has established itself as a highly effective tool for overcoming critical barriers in the development and use of microbial biopreparations. Whole-genome profiling enables a precise identification of genetic determinants that control agronomically significant microbial traits, including phytohormone biosynthesis, diazotrophic activity, inorganic phosphate solubilization, and fungistatic activity against phytopathogens. Targeted selection of promising isolates and the application of genetic editing techniques make it possible to construct strains with optimized functional profiles [27]. Fundamental genomic research elucidates the molecular mechanisms of microflora adaptation to exogenous stressors, facilitating the development of bioagents that maintain high metabolic activity under abiotic and biotic stress [28, 29].

Sinorhizobium bacteria are a successful example of genomic approach to agrobiology. These microorganisms form highly specific symbiotic relationships with legumes (*Fabaceae*), inducing the morphogenesis of root nodules. The bacteria biologically assimilate atmospheric nitrogen inside these structures, converting it into forms bioavailable to the host plant. This process serves as a key source of nitrogen nutrition, minimizing the need for synthetic mineral fertilizers and promoting a more sustainable agricultural production [30]. Advanced genomic research is fundamental to deciphering the complex molecular and cellular cascades underlying the formation and functioning of *Sinorhizobium*–legume symbiotic systems. In particular, they reveal the genes involved in nitrogen fixation, stress resistance, and modulating host–microbe molecular signaling [31]. This review systematizes the current genomic data on *Sinorhizobium* strains, analyzing the molecular determinants of symbiosis with legume plants. In addition, it evaluates the practical integration of these insights into the design of effective bacterial inoculants, thus contributing to the transition toward sustainable agriculture and food security. The overview of the *Sinorhizobium* genomic architecture shows the major symbiosis determinants involved in the biological fixation of essential macro- and micronutrients in the context of sustainable agriculture.

STUDY OBJECTS AND METHODS

The search involved articles published in Scopus, MDPI, ScienceDirect, and Scholar.google between 2001 and 2026. The queries included the following keywords and phrases: *Sinorhizobium*, *agriculture*, *genes*, *nitrogen fixation*, *phosphorus solubilization*, *siderophores*. The search yielded 203 publications that matched the selected keywords, but only 136 records remained after removing duplicates and articles that failed to meet the selection criteria.

Bibliographical data extracted from each publication included the name(s) and surname(s) of the author(s), the headline, the name of the journal, the year of publication, the number of volume or issue, the page interval, and the DOI.

The titles and abstracts were screened to assess their relevance to the research topic. Following the exclusion of 13 irrelevant studies, 123 articles entered the review. The data were exported from the Zotero package in the *.ris* format. The file was processed in VOSviewer to extract keywords in the graphical form. During the processing, 1,163 keywords were extracted from 145 papers, and 56 were selected for further analysis. Figure 1 demonstrates the correlations between these keywords; Figure 2 shows the frequency distribution.

The more often a word occurs, the larger the dot indicating it. The relation between the keywords is color-coded and illustrated with lines.

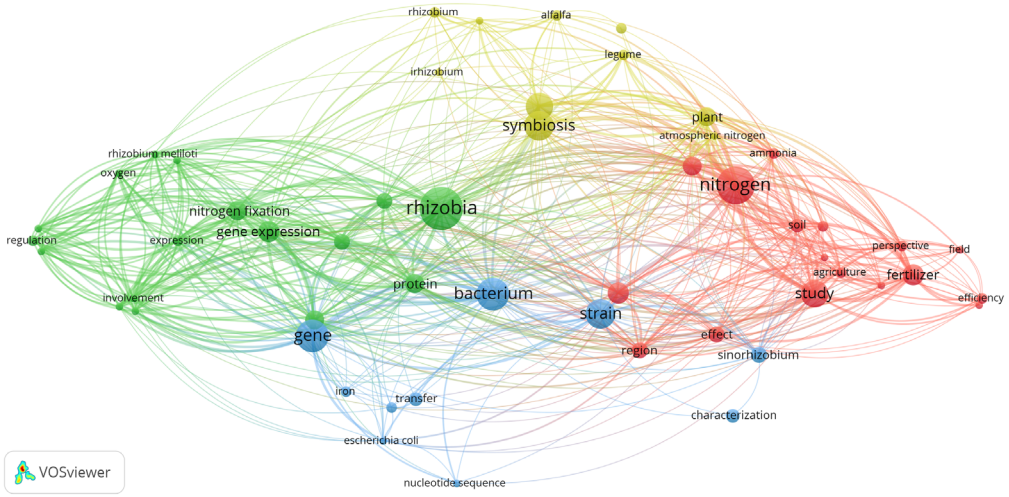

Figure 1 Keyword relationship map

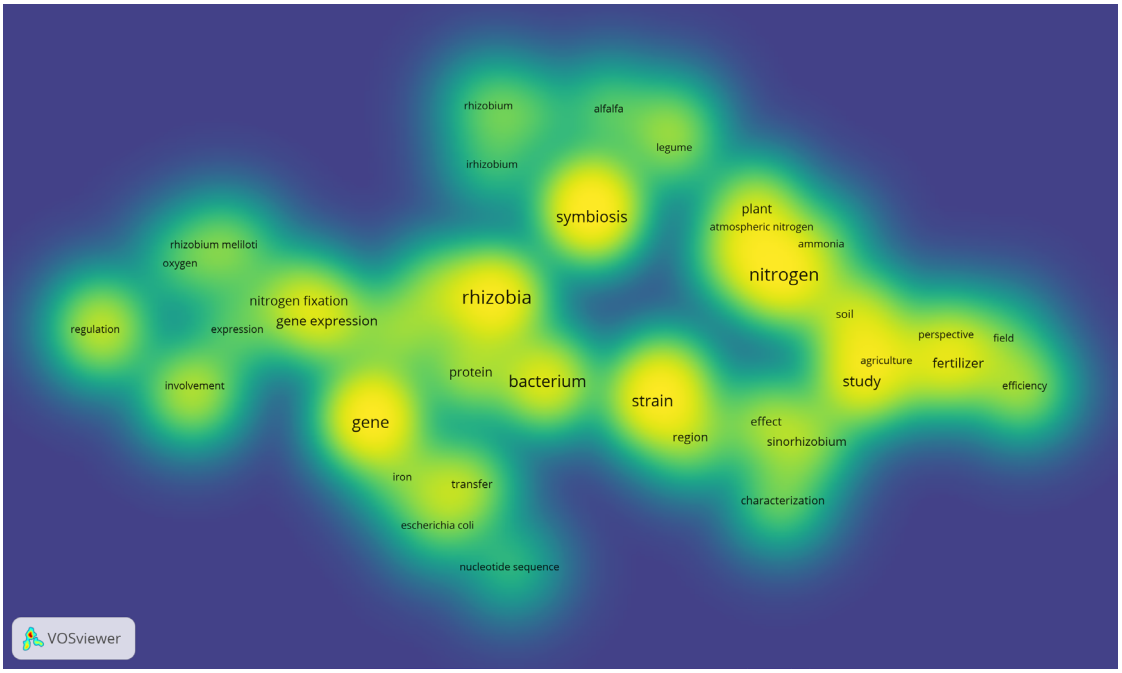

Figure 2 Keyword frequency

The papers from which the most frequent keywords were selected were published in 1993–2025. Figure 3 shows the frequency analysis by publication year.

RESULTS AND DISCUSSION

***Sinorhizobium* (*Ensifer*): Classification and identification challenges.** Rhizobia are an extensive and diverse group of soil bacteria capable of establishing symbiotic relationships with legume plants. As a result of this interaction, specialized structures (nodules) develop on plant roots. They are responsible for biological fixation of atmospheric nitrogen, converting it into a form accessible to plants. The taxonomy of rhizobia is constantly undergoing changes and refinements due to new discoveries [32, 33]. Modern systematics of rhizobia and other bacterial groups follow a polyphase approach, which combines the analysis of phenotypic characteristics and genetic data. Sequencing the 16S ribosomal RNA (rRNA) gene remains the fundamental method of phylogenetic analysis [34].

The group of rhizobia belonging to *Alphaproteobacteria* includes such genera as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Rhizobium*, *Mesorhizobium*, and *Sinorhizobium* [34, 35]. Phylogenetic studies based on 16S rRNA gene analysis revealed a close relationship between the genera *Agrobacterium* and *Allorhizobium* with the genus *Rhizobium* [32]. With no clear phenotypic differences identified, it was proposed to unite these three genera under a single genus, *Rhizobium*. However, this proposal faced significant criticism and remains a subject of ongoing debate within the scientific community [34, 36].

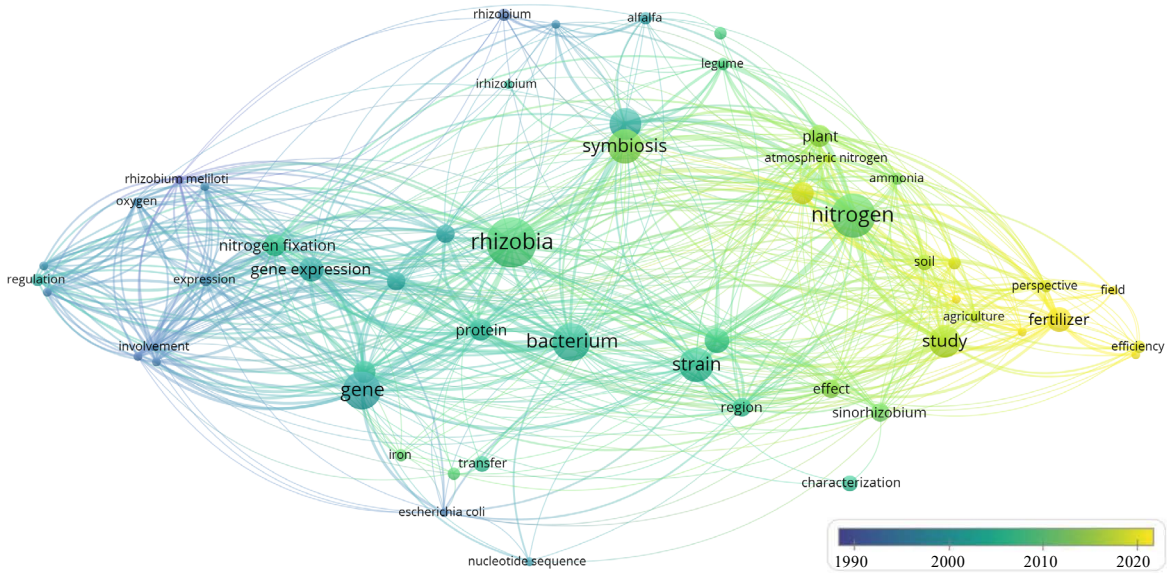

Figure 3 Keyword frequency by year

Initially, the 16S rRNA gene served as a reliable marker for building phylogenetic trees that reflect the evolutionary relationships between organisms [37]. However, a number of recent studies showed that rRNA genes in rhizobia can undergo horizontal gene transfer and recombination, resulting in mosaic DNA sequences [38, 39]. This phenomenon casts doubt on the reliability of those phylogenetic reconstructions that rely solely on the 16S rRNA analysis as it can distort the true evolutionary history. In addition, the high level of conservatism of 16S rRNA gene sequences makes it difficult to distinguish closely related species.

To overcome the limitations associated with the use of 16S rRNA as a phylogenetic marker, protein-coding genes have been increasingly employed in phylogenetic studies [39, 40]. For instance, *recA, gyrB, rpoB, rpoD, groEL*, and *atpD* possess a higher sequence variability compared to rRNA genes. These genes are sufficiently conserved to retain phylogenetic signal while exhibiting greater variability, which makes it possible to design specific primers for their amplification [41]. However, phylogenetic trees constructed using such markers do not always correspond to phylogenies reconstructed from 16S rRNA gene sequences. Such discrepancies may be attributed to horizontal gene transfer, differences in mutation rates across different genes, or stochastic variation. Therefore, multiple molecular markers provide a more reliable phylogenetic reconstruction that takes into account the potential effect of horizontal gene transfer [42, 43].

The genus *Ensifer* (syn. *Sinorhizobium*) represents a convenient model for studying bacterial evolution and functional diversification. It includes both species that form nitrogen-fixing symbioses with legume plants (e. g., *Ensifer meliloti*, *Ensifer fredii*) and those that do not, i. e., the so-called non-symbiotic species (e. g., *Ensifer morelense*, *Ensifer adhaerens*) [44]. The availability of extensive genomic data and a substantial body of experimental studies make members of this genus a promising model system for investigating bacterial symbiosis and adaptation.

In modern taxonomy, the genus *Sinorhizobium* is considered a synonym of the genus *Ensifer*, with *Ensifer* being the priority name according to the rules of bacterial nomenclature. However, both names continue to be widely used in scientific literature, particularly in studies focusing on symbiotic nitrogen-fixing bacteria. The genera *Sinorhizobium* and *Ensifer* were unified due to the high degree of similarity in the 16S rRNA gene and *recA* gene sequences in type strains of these bacteria [45]. This relationship was later supported by a multilocus sequence analysis [43].

However, subsequent phylogenomic studies based on a whole-genome sequence analysis revealed certain discrepancies in the structure of phylogenetic relationships within this group. In particular, *E. adhaerens* was found phylogenetically distant from other members of the combined genus, forming a distinct branch on the phylogenetic tree. Therefore, this species may represent an independent evolutionary lineage [46]. Accordingly, recent phylogenetic reconstructions based on genomic data indicated the need for further refinement of the taxonomic status of this group. The boundaries of the genus *Ensifer* may be changed to exclude some members traditionally assigned to the genera *Ensifer* and *Sinorhizobium* [47].

Despite the phylogenetic division into two distinct clades corresponding to the original genera *Ensifer* and *Sinorhizobium*, the average protein conservation across these groups exceeds 50%. These data was obtained by Kumar *et al*. [48], who observed a similar separation based on the phylogenetic analysis of concatenated sequences of ten conserved genes (*atpD, dnK, gap, glnA, gltA, gyrB, pnp, RecA, rpoB, thrC*). The high levels

of protein conservation suggest a strong degree of genome conservatism, providing evidence for merging the clades into a single genus.

Therefore, the taxonomic classification of *Ensifer* and *Sinorhizobium* remains a complex and controversial task that requires an integrated approach using phylogenomic data, analysis of conserved proteins, and other characteristics.

Symbiotic relationship. The symbiotic interaction between *Sinorhizobium meliloti* and legumes (Fabaceae) represents a complex coevolutionary process characterized by multistep interactions and highly specialized interorganismal communication. This interaction leads to the formation of nodules, which are specialized plant root structures (Fig. 4). They form unique microecological niches in which rhizobia receive carbon-containing compounds from the host plant; their oxidation provides the energy required for biological nitrogen fixation. This process converts atmospheric nitrogen (N_2) into ammonium (NH_4^+), a form of nitrogen available for plant nutrition [49–51].

Initiation of the rhizobia-legume symbiosis begins with the chemotactic recruitment of rhizobia into the host plant rhizosphere mediated by root exudates. Subsequent molecular interactions involve plant and bacterial signaling; they trigger root hair colonization, forming infection threads that penetrate root cortical cells [51]. Bacterial signals induce root cell division and nodule formation, within which rhizobia differentiate into bacteroids. Bacteroids undergo morphological and physiological changes to support nitrogen fixation, a process driven by the activation of genes that encode nitrogenase and other related proteins [50].

The microaerobic environment of the nodule provides optimal conditions for nitrogenase, and it catalyzes the reduction of N_2 to NH_4^+. The host plant supplies bacteroids with carbon-containing compounds necessary to meet the energy costs of the nitrogen fixation process. Therefore, symbiotic nitrogen fixation is a highly coordinated mutualistic exchange of metabolites and signaling molecules between the plant and bacteria [52, 53].

Genetic studies conducted on the *S. meliloti* model and the *M. truncatula* and *Medicago sativa* L. host plants improved the understanding of the molecular mechanisms behind the nitrogen-fixing symbiosis. For instance, *S. meliloti* exopolysaccharides function as critical signaling molecules during infection initiation and thread development [54, 55]. *S. meliloti* synthesizes succinoglycan and galactoglucan, each of which is able to independently maintain symbiotic interactions with the host plant (Fig. 5). Structurally, succinoglycan is a polymer of repeating octasaccharide units, each comprising one galactose and seven glucose residues modified with acetyl, succinyl, and pyruvyl groups [56]. Galactoglucan, in turn, is a polymer of disaccharide subunits that consist of glucose and galactose residues modified with acetyl and pyruvyl groups, respectively [57, 58].

S. meliloti synthesizes and secretes two forms of succinoglycan: a high-molecular-weight form with up to one hundred octasaccharide units; a low-molecular-weight form represented by oligomers that contains from one to three octasaccharide subunits [59].

Among the *S. meliloti* exopolysaccharides, succinoglycan is the best-studied one regarding structure, function, and symbiosis with legumes. *S. meliloti* mutants with impaired biosynthesis, modification, or polymerization of succinoglycan can trigger the early stages of symbiosis, including the deformation of root hairs. However, they exhibit defects in the formation or maintenance of infection threads required to penetrate into the host plant tissues [55].

Mutant *S. meliloti* strains lack the functional ExoY protein, a phosphoglycosyltransferase that initiates succinoglycan biosynthesis. They induce a stronger expression of genes associated with plant defense reactions compared to wild-type bacteria. This observation indicates the potential role of succinoglycan in suppressing the immune response of the host plant [60]. This pheno-

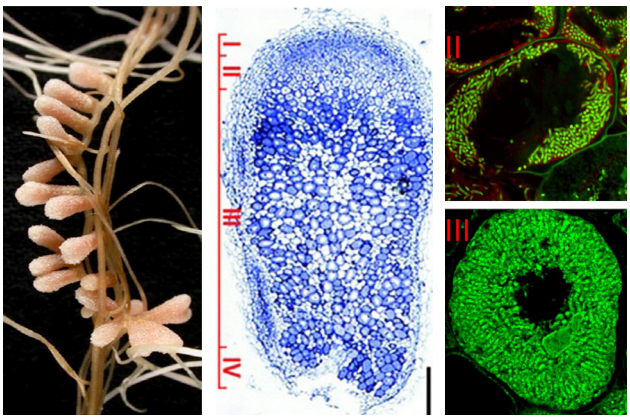

Figure 4 Structure of nitrogen-fixing root nodules formed in *Sinorhizobium meliloti – Medicago truncatula* Gaertn. symbiosis. The different nodule zones are indicated on the longitudinal nodule section: (I) meristem; (II) infection zone; (III) nitrogen fixation zone; and (IV) senescence zone. Symbiotic cells in zone II contain the differentiating endosymbionts while in zone III the host cytoplasm is fully packed with long nitrogen-fixing bacteroids. Endosymbionts stained with Syto9 have green fluorescence [52]

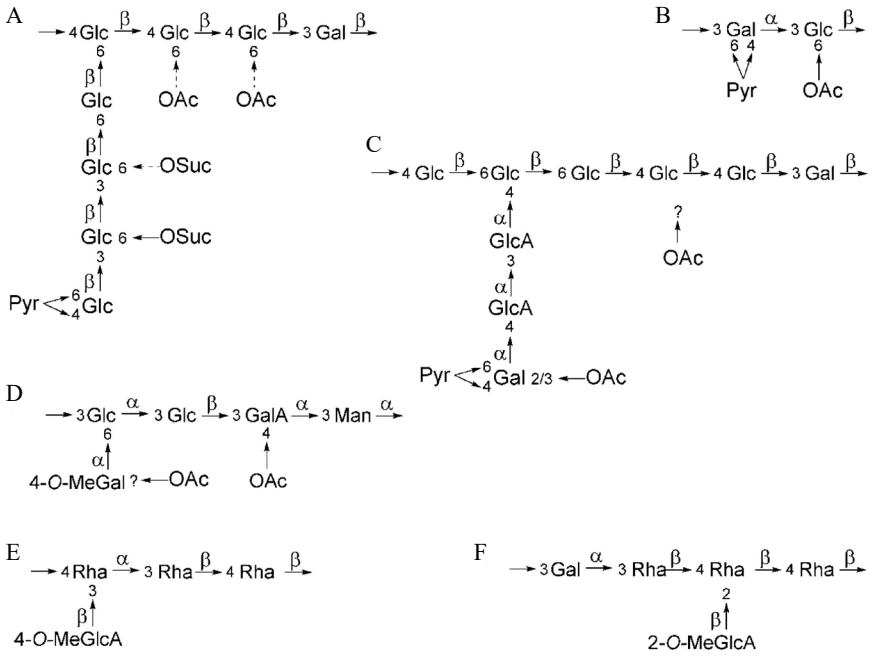

Figure 5 Structure of exopolysaccharides (EPS) and non-starch polysaccharides (NPS) produced by different sino- and radyrhizobia: *Sinorhizobium meliloti* 1021 EPS I (A) and II (B); *Sinorhizobium fredii* HH103 and NGR234 EPS (C); *Bradyrhizobium japonicum* USDA110 EPS (D); *Bradyrhizobium elkanii* USDA61 EPS/NPS (E); and *Bradyrhizobium japonicum* USDA110 NPS (F). Dashed arrows indicate partial substitutions while α and β stand for α- and β-glycosidic linkages, respectively. The position of the *O*-acetyl group is unknown [58]

type confirms the hypothesis that succinoglycan functions as a signaling molecule recognized by the plant. Kawaharada *et al*. [61, 62] provided direct evidence for this hypothesis by identifying a host plant receptor specifically binding to bacterial exopolysaccharides. The interaction of exopolysaccharides with this receptor triggers the growth of the infectious thread and ensures the penetration of bacteria through the epidermal root layers. Beyond its role in the early stages, succinoglycan is essential for the late stages of symbiotic interactions [63, 64].

Symbiotic nitrogen fixation requires a suite of molecular functions in bacteria, including signaling pathways for host communication, coordinated metabolism, a functional nitrogenase complex, and mechanisms to avoid or suppress plant immunity [50]. The key genes required for symbiotic nitrogen fixation (*nod, nif, fix*) are often localized in mobile genetic elements, such as symbiotic islands and megaplasmids, which promotes their spread through a horizontal gene transfer [65].

Investigating the mutualistic metabolic and genetic contributions to the evolution of mutualistic symbioses is a pivotal research area, particularly regarding the symbiotic nitrogen fixation. Along with the genes directly determining the symbiotic phenotype, non-symbiotic genes are also essential for this interaction [65–67].

Experimental data demonstrate the effect of rhizobia on the interaction with legumes. The transformation of phylogenetically close non-symbiotic species of genera *Agrobacterium* and *Ensifer* by symbiotic plasmids isolated from *Rhizobium* or *Ensifer* (*Sinorhizobium*) rhizobia fails to establish effective symbiotic relationships [45]. Similarly, the same symbiotic island is associated with completely different symbiotic phenotypes depending on the *Mesorhizobium* genotype [68]. Thus, the successful nitrogen fixation depends not only on the core symbiotic genes, but also on the coevolution and adaptation of the metabolic and regulatory networks of the bacterial partner.

Fixation of atmospheric nitrogen. The regulation mechanisms of symbiotic nitrogen fixation depend on the type of rhizobia. The *S. meliloti* system is one of the most studied regulation models of symbiotic nitrogen fixation. The complete sequencing of *S. meliloti* strain 1021 marked a milestone in genomics. This strain comprises a 3.65 Mb chromosome and two megaplasmids (*pSymA*, 1.36 Mb; *pSymB*, 1.68 Mb) [69]. The accumulated experimental data obtained using high-throughput methods [70] provided a robust framework for the systematic analysis of the *S. meliloti* metabolic potential. Computer simulation of metabolic processes (metabolic reconstruction *in silico*) has become an important tool for identifying key genes responsible for the symbiotic fixation in this species.

The genetic basis for nodule organogenesis and nitrogen fixation can be attributed to core genes, including *nod, nif*, and *fix* [71]. The horizontal transfer of these genes is critical for symbiosis. It initiates the formation of symbiotic functionality in phylogenetically diverse bacteria belonging to *α*- and *β*-proteobacteria [72, 73]. Table 1 contains a list of genes responsible for the atmospheric nitrogen fixation (National Library of Medicine).

Table 1 Nitrogen fixation genes in the genus *Sinorhizobium*

Name	Gene ID	Organism	Aliases
nifA	61614849	*Sinorhizobium medicae*	FB009_RS30680, FB009_1359
nifA	48977623	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32475, AOX55_00004465
nifA	89573862	*Sinorhizobium meliloti*	V7S97_RS07390, V7S97_001467
nifH	25012506	*Sinorhizobium meliloti* GR4	C770_RS23810, C770_GR4pC1039
nifH	61614856	*Sinorhizobium medicae*	FB009_RS30730, FB009_13515
nifH	48977766	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS33285, AOX55_00004623
nifH	48977636	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32540, AOX55_00004479
nifH	89573868	*Sinorhizobium meliloti*	V7S97_RS07420, V7S97_001473
nifD	61614857	*Sinorhizobium medicae*	FB009_RS30735, FB009_13516
nifD	48977765	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS33280, AOX55_00004622
nifD	89573869	*Sinorhizobium meliloti*	V7S97_RS07425, V7S97_001474
nifK	61614858	*Sinorhizobium medicae*	FB009_RS30740, FB009_13517
nifE	48977639	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32555, AOX55_00004482
nifE	89573871	*Sinorhizobium meliloti*	V7S97_RS07435, V7S97_001476
nifN	61615013	*Sinorhizobium medicae*	FB009_RS31670, FB009_14210
nifN	89573899	*Sinorhizobium meliloti*	V7S97_RS07575, V7S97_001504
nifN	48977640	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32560, AOX55_00004483
nifW	48977610	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32390, AOX55_00004447
nifX	89573872	*Sinorhizobium meliloti*	V7S97_RS07440, V7S97_001477
nifB	89573861	*Sinorhizobium meliloti*	V7S97_RS07385, V7S97_001466
nodA	61615011	*Sinorhizobium medicae*	FB009_RS31655, FB009_1428
nodA	48977543	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32015, AOX55_00004375
nodA	89573897	*Sinorhizobium meliloti*	V7S97_RS07565, V7S97_001502
nodB	61615010	*Sinorhizobium medicae*	FB009_RS31650, FB009_1427
nodB	48977544	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32020, AOX55_00004376
nodB	89573896	*Sinorhizobium meliloti*	V7S97_RS07560, V7S97_001501
nodC	61615009	*Sinorhizobium medicae*	FB009_RS31645, FB009_1426
nodC	48977545	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32025, AOX55_00004377
nodC	89573895	*Sinorhizobium meliloti*	V7S97_RS07555, V7S97_001500
nodD2	61614787	*Sinorhizobium medicae*	FB009_RS30305, FB009_1331
nodD1	61615012	*Sinorhizobium medicae*	FB009_RS31660, FB009_1429
nodD3	61614870	*Sinorhizobium medicae*	FB009_RS30810, FB009_13529
nodD1	48977680	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS32790, AOX55_00004529
nodD2	48977753	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS33210, AOX55_00004607
fixL	89572460	*Sinorhizobium meliloti*	V7S97_RS00380, V7S97_000076
fixL	61615116	*Sinorhizobium medicae*	FB009_RS32290, FB009_1517
fixJ	61615117	*Sinorhizobium medicae*	FB009_RS32295, FB009_1518
fixJ	25011576	*Sinorhizobium meliloti* GR4	C770_RS22470, C770_GR4pC0725
fixJ	89572459	*Sinorhizobium meliloti*	V7S97_RS00375, V7S97_000075
fixJ	25012162	*Sinorhizobium meliloti* GR4	C770_RS23990

Bacteroids regulate symbiotic nitrogen fixation using a complex network of interacting factors, e. g., the oxygen-sensitive two-component FixL/FixJ system, the transcription factor NifA, the Σ-factor σ54, the FixK regulator, etc. [70]. These regulatory proteins control the expression of genes involved in the bacteroid differentiation and adaptation to a symbiotic lifestyle [74].

Under conditions of micro-aerobiosis, FixL kinase activates and phosphorylates the Fix regulatory protein, thus initiating a cascade of signal transmission. The phosphorylated Fix activates the transcription of genes encoding nitrogen fixation regulators, including NifA and FixL itself. Structurally, the FixL protein consists of two main domains. The N-terminal domain is represented by a Per-Arnt-Sim (PAS) sensor module containing a heme-binding site responsible for oxygen detection [75]. The C-terminal domain possesses its own histidine kinase activity; it includes a catalytic ATP-binding domain and a phosphotransfer domain for histidine [76]. Thus, FixL functions as an oxygen sensor and signal transducer, regulating the expression of nitrogen fixation genes in response to changes in oxygen concentration in the environment.

Transcriptomic changes in bacteroids include suppression of most metabolic pathways, coupled with simultaneous activation of genes essential for nitrogen fixation and respiration [71]. Increased respiratory activity provides nitrogenase with the necessary amount of energy (16 ATP molecules) and reducing equivalents (8 electrons) to convert one N_2 molecule to two molecules of NH_4^+ [77].

As a product of the nitrogenase activity, ammonium (NH_4^+) is secreted by bacteroids and transported to plant cells through specialized ammonium channels localized in the peribacteroid membrane. A complex system of amino acid exchange between symbionts prevents NH_4^+ assimilation by bacteroids [78]. This mechanism directs the assimilated nitrogen flow to the host plant.

Producing siderophores. Iron is an essential trace element necessary for the vital activity of most organisms, and it acts as a common resource in various ecological niches. Despite its abundance in biosphere, iron bioavailability is limited by the predominance of the oxidized forms, especially trivalent iron (Fe^{3+}) with its low solubility at neutral and alkaline pH values.

Iron metabolism is critical for the nitrogen-fixing activity of rhizobia that live intracellularly in the root nodules of leguminous plants [79]. Nitrogenase, a key nitrogen fixation enzyme, contains iron-sulfur [4Fe-4S] and [8Fe-7S] clusters, as well as the iron-molybdenum cofactor $MoFe_7S_9$ homocitrate (Fig. 6). In addition, leghemoglobin, a heme-containing protein, maintains microaerobic conditions within nodules to support nitrogenase activity. At the same time, leghemoglobin facilitates a high flux of oxygen at low free concentrations, preventing its inactivation while ensuring bacteroid respiration [80]. The Irr protein, which regulates iron metabolism, is active in iron deficiency conditions. In iron excess conditions, it is inactivated either by the heme-mediated degradation, or by the dissociation from DNA, depending on the species [81, 82].

To assimilate trivalent iron (Fe^{3+}), many bacteria use a mechanism based on the production of siderophores, low-molecular-weight and high-affinity Fe^{3+} chelators. Siderophores form soluble complexes with Fe^{3+}, which are then actively transported into the cell through specific receptors of the outer membrane in Gram-negative bacteria. Due to ABC transporters, they are present in both Gram-negative and Gram-positive bacteria. The siderophore biosynthesis occurs exclusively in iron deficiency conditions and is negatively regulated by the Fur repressor protein in complex with iron. Many structurally diverse siderophores have been identified in various strains of rhizobia [83, 84].

In *S. meliloti*, the absorption of ferriciderophores is mediated by specific receptor proteins localized in the outer membrane. In addition, some bacteria are able to absorb iron using exogenous siderophores, such as those produced by fungi [85]. Many strains of nodule bacteria, both fast- and slow-growing species, fail to synthesize high-affinity iron chelators. Table 2 contains a list of genes responsible for the synthesis of siderophores (National Library of Medicine).

Rhizobactin is the most genetically studied siderophore produced within the genus *Sinorhizobium*. The transcription of rhizobactin biosynthesis and transport genes in strain 1021 depends on the iron concentration, which corresponds to the typical mechanism of siderophore regulation mediated by the Fur protein [86].

In addition to the iron-dependent regulation, the rhizobactin biosynthesis and transport (e. g., *Sinorhizobium meliloti* 1021) are controlled by the AraC-like transcription activator RhrA. The CAS analysis detected neither siderophore production in *rhrA* mutants nor expression of the *rhtA* outer membrane receptor [86]. The ribonuclease protection assay detected low levels of *rhbA* and *rhtA* mRNAs, confirming that, in iron deficiency conditions, the rhizobactin biosynthesis and transport depend on the transcriptional activation mediated by RhrA.

RhrA is homologous to AraC-type regulators, including PchR, YbtA, and AlCr, which activate the expression of pyochelin biosynthesis and transport genes in *Pseudomonas aeruginosa*, yersiniabactin in *Yersinia pestis* [87].

Phosphorus transport. Phosphorus is an essential macronutrient for plants, introduced into the soil as soluble inorganic phosphates. However, these phosphates are prone to immobilization, turning into insoluble forms that are inaccessible for assimilation by agricultural crops [88]. As a result, phosphorus is often a limiting factor in plant growth [89]. It is essential for various metabolic processes and is part of important biomolecules, e. g., in alfalfa. Soluble phosphorus deficiency is widespread in soils all over the world. Even in fertile soils, the concentration of phosphorus available to plants is usually low due to its high reactivity with calcium, iron, and aluminum, which leads to the formation of insoluble compounds and phosphorus deposition [90].

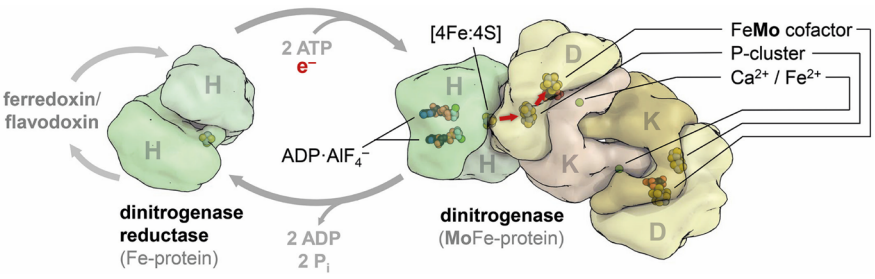

Figure 6 Components of nitrogenase system and their interaction. A low-potential ferredoxin of flavodoxin reduces the reductase component (Fe protein), which then binds 2 ATP and undergoes a conformational change that allows for a complex formation with the dinitrogenase component. This phenomenon triggers the ATP hydrolysis: an electron is transferred from the [8Fe:7S] P-cluster to the active-site cofactor, a [Mo:7Fe:9S:C]:homocitrate cluster in the case of Mo-nitrogenase (red arrows). The reduction of a single N_2 molecule to 2 NH_4^+ requires this cycle to be repeated eight times at the expense of 16 ATP [82]

Table 2 Siderophore synthesis and iron regulation genes in the genus *Sinorhizobium*

Name	Gene ID	Organism	Aliases
mucR	61609890	*Sinorhizobium medicae*	FB009_RS04555, FB009_102245
rirA	48971869	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS01920, AOX55_0000409
rirA	89575044	*Sinorhizobium meliloti*	V7S97_RS13300
rirA	29518561	*Ensifer adhaerens*	FA04_RS01765, FA04_01765
FB009_RS23505	61613517	*Sinorhizobium medicae*	FB009_RS23505, FB009_11611
FB009_RS07780	61610500	*Sinorhizobium medicae*	FB009_RS07780, FB009_10419
AOX55_RS17075	48974737	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS17075, AOX55_00003527
AOX55_RS09920	48973381	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS09920, AOX55_00002078
V7S97_RS19305	89576245	*Sinorhizobium meliloti*	V7S97_RS19305
V7S97_RS08305	89574045	*Sinorhizobium meliloti*	V7S97_RS08305
NEWENTRY	2831197	*Sinorhizobium meliloti* 1021	–
irrA	61611002	Sinorhizobium medicae	FB009_RS10365, FB009_105145
irrA	48975246	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS19685, AOX55_00004078
FA04_RS08475	29520338	*Ensifer adhaerens*	FA04_RS08475, FA04_08455
FA04_RS16435	29517633	*Ensifer adhaerens*	FA04_RS16435, FA04_16410
irrA	29517489	*Ensifer adhaerens*	FA04_RS18835, FA04_18805
rhbA	89573403	*Sinorhizobium meliloti*	V7S97_RS05095, V7S97_001015, rhsA
rhbB	89573404	*Sinorhizobium meliloti*	V7S97_RS05100
rhbC	89573405	*Sinorhizobium meliloti*	V7S97_RS05105, V7S97_001017, rhsC
C770_RS19225	25011522	*Sinorhizobium meliloti* GR4	C770_RS19225, C770_GR4pC0041
FA04_RS20000	29521998	*Ensifer adhaerens*	FA04_RS20000, FA04_19970
FA04_RS20005	29520710	*Ensifer adhaerens*	FA04_RS20005, FA04_19975
rhbD	89573406	*Sinorhizobium meliloti*	V7S97_RS05110, V7S97_001018, rhsD
C770_RS19220	25011481	*Sinorhizobium meliloti* GR4	C770_RS19220, C770_GR4pC0040
C770_RS19215	25011899	*Sinorhizobium meliloti* GR4	C770_RS19215, C770_GR4pC0039
rhbF	89573408	*Sinorhizobium meliloti*	V7S97_RS05120, V7S97_001020, rhsF
C770_RS19210	25012289	*Sinorhizobium meliloti* GR4	C770_RS19210, C770_GR4pC0038
FB009_RS11740	61611269	*Sinorhizobium medicae*	FB009_RS11740, FB009_1069

Studying the mechanisms of phosphorus uptake by various microorganisms showed that many bacterial species, including *S. meliloti*, have at least two phosphorus transport systems: high-affinity and low-affinity ones. High-affinity transport is encoded by the *phoCDET* operon, and low-affinity transport is encoded by the *pit* gene (as part of the *orfA-pit* operon). In *S. meliloti*, the expression of genes of both phosphorus transport systems is regulated by the PhoB activator. If phosphorus is abundant, PhoB remains inactive, and the *phoCDET* genes are not expressed. Under phosphorus deficiency, the activated PhoB suppresses low-affinity transport by Pit permease and simultaneously induces the expression of the high-affinity *phoCDET* system, which becomes the main mechanism of phosphorus transport [91]. Table 3 demonstrates the genes associated with phosphorus transport in *Sinorhizobium*.

Many bacterial strains contain *pstSCAB* homologues that function as high-affinity phosphate transporters. In *S. meliloti* 1021, deletion of one nucleotide in the open reading frame of *pstC* led to a moderate constitutive activation of 12 phosphorus-starvation-induced genes (via PhoB), even in the absence of phosphorus stress [92]. In both plants and microorganisms, proton (H^+) release, organic acid production, and acid phosphatase biosynthesis are the main mechanisms for increasing phosphorus availability [93].

Organic acids include acetate, lactate, malate, oxalate, succinate, citrate, gluconate, ketogluconate, etc. They are capable of forming complexes with iron or aluminum in iron and aluminum phosphates, thus releasing a phosphate available to plants [94]. Organic acids can also increase the phosphorus availability by blocking phosphorus binding sites on soil particles or by forming complexes with cations on the surface of soil minerals [95].

Zinc transport. Zinc (Zn), an essential trace element for all living organisms, serves as a catalytic cofactor and structural component in a vast array of proteins [96]. Bacteria maintain zinc homeostasis within tightly regulated limits to ensure optimal growth and survival. This homeostasis is achieved through the coordinated operation of systems governing Zn absorption, intracellular distribution, and export, which are controlled by specialized regulatory proteins [97]. In most bacterial species, the availability of Zn is regulated by the protein Zur, a member of the well-characterized family of Fur regulators. Zur functions as a repressor of genes involved in Zn transport into the cell, acting as a key regulator of Zn homeostasis [98, 99]. However, Zn uptake systems vary significantly in the number, organization, and functional characteristics across different genomic contexts, which can significantly complicate the mechanisms of regulation.

The ZnuABC transport system is crucial for bacterial growth under conditions of zinc deficiency, and it

Table 3 Phosphorus transport genes in the genus *Sinorhizobium*

Name	Gene ID	Organism	Aliases
FB009_RS08105	61610564	*Sinorhizobium medicae*	FB009_RS08105, FB009_10484
AOX55_RS17545	48974825	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS17545, AOX55_00003618
FA04_RS31685	29523222	*Ensifer adhaerens*	FA04_RS31685, FA04_31635
FA04_RS16750	29517451	*Ensifer adhaerens*	FA04_RS16750, FA04_16725
FB009_RS04020	61609787	*Sinorhizobium medicae*	FB009_RS04020, FB009_102139
AOX55_RS02990	48972073	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS02990, AOX55_0000634
FB009_RS10850	61611095	*Sinorhizobium medicae*	FB009_RS10850, FB009_105235
AOX55_RS20150	48975334	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS20150, AOX55_00004170
FA04_RS19450	29518331	*Ensifer adhaerens*	FA04_RS19450, FA04_19420
FA04_RS02660	29517118	*Ensifer adhaerens*	FA04_RS02660, FA04_02655
pstC	61611249	*Sinorhizobium medicae*	FB009_RS11635, FB009_105388
pstC	48971670	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS00905, AOX55_0000189
pstC	89574830	*Sinorhizobium meliloti*	V7S97_RS12230
pstC	29516724	*Ensifer adhaerens*	FA04_RS00715, FA04_00715
pstA	61611250	*Sinorhizobium medicae*	FB009_RS11640, FB009_105389
pstA	48971671	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS00910, AOX55_0000190
pstA	89574831	*Sinorhizobium meliloti*	V7S97_RS12235
pstA	29520235	*Ensifer adhaerens*	FA04_RS00720, FA04_00720
pstB	89574832	*Sinorhizobium meliloti*	V7S97_RS12240
pstB	61611251	*Sinorhizobium medicae*	FB009_RS11645, FB009_105390
pstB	48971672	*Sinorhizobium fredii* CCBAU 25509	AOX55_RS00915, AOX55_0000191
pstB	29518188	*Ensifer adhaerens*	FA04_RS00725, FA04_00725

Table 4 Zinc transport genes of genus *Sinorhizobium*

Name	Gene ID	Organism	Aliases
znuA	48973384	*Sinorhizobium fredii*	AOX55_RS09935, AOX55_00002081
znuA	89576248	*Sinorhizobium meliloti*	V7S97_RS19320
znuA	29520304	*Ensifer adhaerens*	FA04_RS08490, FA04_08470
FB009_RS23520	61613520	*Sinorhizobium medicae*	FB009_RS23520, FB009_11614
znuB	89576246	*Sinorhizobium meliloti*	V7S97_RS19310
znuB	61613518	*Sinorhizobium medicae*	FB009_RS23510, FB009_11612
znuB	48973382	*Sinorhizobiumfredii* CCBAU 25509	AOX55_RS09925, AOX55_00002079
FB009_RS07800	61610504	*Sinorhizobium medicae*	FB009_RS07800, FB009_10423
FB009_RS07795	61610503	*Sinorhizobium medicae*	FB009_RS07795, FB009_10422
AOX55_RS17095	48974741	*Sinorhizobium fredii*	AOX55_RS17095, AOX55_00003531
AOX55_RS17090	48974740	*Sinorhizobium fredii*	AOX55_RS17090, AOX55_00003530
FA04_RS16450	29517627	*Ensifer adhaerens*	FA04_RS16450, FA04_16425
FA04_RS16455	29517625	*Ensifer adhaerens*	FA04_RS16455, FA04_16430

affects their virulence in various species [100]. However, this correlation is not universal. For instance, inactivation of the *znuABC* gene in *Y. pestis* fails to reduce virulence, despite ZnuABC functioning as the primary high-affinity zinc importer. Conversely, in *Agrobacterium tumefaciens* (Smith et Townsend) Conn., zinc uptake is primarily mediated by the TroCBA transport system rather than ZnuABC [99, 101]. In *Escherichia coli* and *Salmonella enterica*, the ZinT protein appears to assist ZnuA in zinc transport [102].

Lu *et al*. [103] studied deletion mutants of five genes encoding P1B-type ATPases in *S. meliloti* strain CCNWSX0020. The *zntA* mutant exhibited significantly increased sensitivity to low concentrations of zinc and cadmium ions compared to other mutant strains and the wild-type (non-mutant) strain. This finding indicates a key role for the ZntA protein, conferring resistance to the toxic effects of Zn and Cd in *S. meliloti* (Table 4).

In *A. tumefaciens*, ZinT seems to interact primarily with the dominant TroCBA high-affinity carrier rather than ZnuA. Zinc homeostasis has been extensively studied in pathogenic bacteria, but the role of these mechanisms in establishing beneficial interactions with plants remains largely unknown [104].

The *znuABC* genes of the *Sinorhizobium fredii* CCBAU45436 strain possesses a broad host range. They exhibit increased expression in the nodules of both cultivated soybean (*Glycine max* (L.) Merr.) and wild soybean (*Glycine soja* Siebold & Zucc.), compared to free-living rhizobia cells grown on a nutrient-rich medium. As a result, the environment within the nodules restricts zinc availability for rhizobia. When the *znuA* gene was

eliminated from *S. fredii* CCBAU45436, it resulted in the development of functionally inactive nodules in the varieties *G. max* JD17 and C08, as well as in a lower number of active nodules in *G. soja* W05 [105, 106].

The soybean zinc transporter GmZIP1 is localized on the membrane of the symbiosome, which houses nitrogen-fixing rhizobia, or bacteroids, within nodule cells. Isolated soybean symbiosomes actively uptake zinc from their surroundings [107]. Likewise, suppressed expression of MtZIP6, a zinc transporter, in alfalfa (*M. truncatula*) resulted in a lower nitrogenase activity, as well as a reduction in both the quantity of pink (nitrogen-fixing) nodules and the overall biomass of the plant [108]. These findings indicate the pivotal significance of zinc assimilation in the symbiotic relationship between rhizobia and leguminous plants, from nodule organogenesis to active nitrogen fixation.

In *S. meliloti* CCNWSX0020, the *zntA* and *copA1b* genes that encode P1B-type ATPases are involved in conferring cellular resistance to Zn^{2+}. The *zntA* gene belongs to the P1B-2 subfamily and is associated with the transport of Zn^{2+}, Cd^{2+}, and Pb^{2+}. *CopA1b* belongs to the P1B-1 ATPases, which are linked to the transport of Cu^{+}/Ag^{+}. Nevertheless, both proteins, ZntA and CopA1b, protect cells against the toxic effects of Zn^{2+} and other heavy metals. According to Lu *et al*. [103], deletions of *zntA* and *copA1b* raised the sensitivity to Zn^{2+}, Cd^{2+}, and Pb^{2+} compared to the wild-type strain. Mutations in other P1B-type ATPase genes (*fixI1, copA3, nia*) produced no such effect. Obviously, ZntA and CopA1b are crucial in maintaining zinc homeostasis in *S. meliloti*.

***Sinorhizobium* bacteria in agriculture.** *Sinorhizobium* strains have demonstrated high efficacy in boosting crop productivity. For example, Ivanova & Skalozub [109] reported that the treatment of alfalfa with *S. meliloti* increased the yield of green mass and dry matter by 7–22%. In other study [110], inoculation with *S. meliloti* stimulated the growth of shoots and roots of *Melilotus officinalis* (L.) Lam. by more than 75% in soil supplemented with regolith.

In addition to nitrogen fixation, *Sinorhizobium* strains have other valuable properties that contribute to the sustainability of agroecosystems. In particular, *Sinorhizobium saheli* YH1 could reduce the toxicity of heavy metals in soil, protecting *Leucaena leucocephala* (Lam.) de Wit from their negative effects. *S. saheli* also accumulated significant amounts of chromium and exhibited high tolerance to nickel and cadmium [111]. The *S. saheli* isolated by Oves *et al*. [112] demonstrated the ability to accumulate 91% m/m chromium, depending on the amount of metal introduced into the nutrient medium. It also accumulated up to 1,000 μg/mL nickel and 250 μg/mL cadmium (Cd) [113]. This finding opens up prospects for the use of *Sinorhizobium* in phytoremediation of polluted soils.

Certain *Sinorhizobium* strains are highly tolerant to various abiotic stress factors, including drought, high soil salinity, and extreme temperature fluctuations. This ability to survive and maintain metabolic activity under adverse conditions makes these microorganisms promising agents for the restoration and stabilization of ecosystems exposed to abiotic stress, particularly in arid and semi-arid regions [111].

For instarnce, *S. meliloti* was reported to enhance the yield of *Medicago sativa* L. under salt stress conditions [113]. Strains isolated by Sijilmassi *et al*. [114] exhibited tolerance to drought and salinity. They also had a wide range of plant growth-promoting properties, including phytohormone production. In particular, *Rhizobium tropici* CIAT 899 demonstrated tolerance to both salinity (5% NaCl) and drought ($\psi = -2.6$ MPa), whereas *R. tropici* 686N5 exhibited high salt tolerance (5% NaCl) and moderate drought tolerance ($\psi = -0.75$ MPa).

Due to their adaptive properties, *Sinorhizobium* strains can be applied in sustainable agricultural strategies. In addition to enhancing crop yields, they improve the physicochemical properties of soils, restoring their fertility and reducing negative impacts on ecosystems under abiotic stress conditions.

Future perspectives. The review made it possible to identify several promising research directions related to the use of *Sinorhizobium* strains in sustainable agricultural systems. One such direction is the study of genetic determinants regulating the processes of symbiotic nitrogen fixation and bacterial adaptation to adverse environmental conditions. In recent years, targeted genome editing methods, including CRISPR–CAS systems, have been actively applied for the functional analysis of rhizobial genes [113, 115]. In particular, precise genome editing tools developed for *S. meliloti* now allow for point mutations and multiplexed gene modification. These capabilities significantly accelerate functional genomics concerning symbiosis and bacterial metabolism [116].

Another important research direction features the molecular mechanisms underlying symbiotic interactions between *Sinorhizobium* and legume plants. These mechanisms involve a complex system of signaling exchange between the plant and the bacterium during the early stages of root infection. For example, flavonoids secreted by plant roots activate NodD regulatory proteins in rhizobia, leading to the synthesis of Nod factors, i. e., signaling molecules that initiate the formation of infection threads and nodule organogenesis [117]. In addition, bacterial exopolysaccharides and type III secretion system proteins serve as critical determinants of host-strain compatibility and nodule formation in specific plant genotypes. According to transcriptomic studies of soybean roots, variations in the NopP and NopI proteins in *Sinorhizobium fredii* could significantly alter the specificity of symbiotic interactions [118]. Such findings contribute to a deeper understanding of symbiosis formation mechanisms and are considered a basis for the development of more effective microbial inoculants.

Recent years have seen significant advancements in rhizosphere microbiome research, driven by metagenomics and other high-throughput molecular technologies. Metagenomic analysis can identify the functional genes involved in biogeochemical cycles, including

genes associated with the mobilization of phosphorus, nitrogen, and carbon. Such studies demonstrate that rhizosphere microorganisms are crucial for the formation of bioavailable nutrient forms, as well as for maintaining stable soil ecosystems [119].

Contemporary research confirms the high biotechnological potential of *Sinorhizobium* strains for sustainable agriculture. However, their practical application depends on a complex set of interrelated factors, including the genetic characteristics of strains, the physicochemical properties of the soil substrate, the structure of microbial consortia, and the specific features of regional climatic conditions.

CONCLUSION

Genomic profiling of *Sinorhizobium* microorganisms catalyses the development of sustainable agricultural production. Identifying the key genetic determinants of nitrogen-fixing symbiosis and phosphorus bioavailability provides opportunities for the development of innovative biopreparations that increase crop yield without the extensive use of agrochemicals. Studying the synergies between *Sinorhizobium* and associated rhizosphere microflora expands the methodological toolkit for advanced adaptive landscape farming practices [78, 112]. These methodological approaches are aimed at developing a functionally stable and balanced soil microbiome while prolonging the resistance of agrophytocenoses to phytopathogens and insect pests. This protective potential is realized through mechanisms of interspecific competition for nutrients, the biosynthesis of antimicrobial metabolites, and the activation of induced systemic resistance in plants [120–122]. Together, these processes improve phytosanitary conditions and increase the adaptive potential of agroecosystems under concomitant biotic and abiotic stressors.

When integrated into the study of rhizosphere ecosystems, metagenomic technologies open up unique opportunities for the systematic analysis of functionally diverse growth-promoting microorganisms and their interfering relationships. A metagenomic analysis can identify new genetic loci and metabolic pathways that mediate the communication between *Sinorhizobium* bacteria, the host plant, and associated components of the rhizosphere microbiota. A genome-wide analysis of the microbiome and uncultivated forms provides a complete picture of the full functional potential of the biocenosis.

Metagenomic profiling makes it possible to identify the genes that encode symbiotic proteins responsible for biological nitrogen fixation, phytohormone biosynthesis, and other key processes in plant ontogenesis. Furthermore, this approach facilitates the mapping of metabolic pathways that support nutrient cycling, organic matter degradation, and xenobiotic degradation, which are essential for maintaining soil ecological homeostasis.

Based on the analytical data obtained, agricultural scientists can develop new strategies for targeted modulation of the microbiome structure and functions to optimize crop yield and stress tolerance. Such solutions provide a scientific and technological framework for the design of highly effective multifunctional microbial preparations that promote the development of resilient agroecosystems and ensure stable crop yields under climate fluctuations.

Genomic markers make it possible to monitor the state of *Sinorhizobium* communities, opening up opportunities for analyzing their symbiotic effectiveness and trophic interactions with plants under changing environmental conditions. By identifying patterns in the functioning of these taxa, agricultural scientists may learn to regulate the rhizosphere microbiome, thus optimizing the beneficial interspecies interactions. An in-depth study of *Sinorhizobium* genomics is a strategic factor in intensifying sustainable agriculture, ensuring synergy between highly productive agrocenoses and minimizing the human-induced impact on the biosphere.

These findings may lead to new strategies for tailoring the structure and functioning of the rhizosphere microbiome in order to optimize its beneficial properties for plants. The accumulated knowledge about the *Sinorhizobium* genome makes it possible to design new strains with tailored properties. Research in this field is currently progressing rapidly. For example, scientists were able to remove the *ku* gene involved in the nonhomologous end joining (NHEJ) from the CRISPR/Cas12 eGET system in *Sinorhizobium meliloti* SM320 [123]. While enhancing the efficiency of homologous recombination, this achievement will be useful for metabolic engineering and basic SM320 research. Furthermore, it may provide a platform for the development of CRISPR/CAS systems in strains with low homologous recombination efficiency. This approach opens up prospects for targeted modification of the *Sinorhizobium* genome to tailor strains with increased nitrogen-fixing activity, ability to mobilize phosphorus and other nutrients, and high resistance to stress factors.

The strategy of integrating genomic information with rhizosphere management may reduce the dependence on mineral fertilizers. It seems particularly relevant in the context of global climate change, which increases the stress on agricultural crops. However, its implementation requires systematic field evaluations, regulatory assessment, and novel, commercially viable formulations.

The review indicates a significant potential of synthetic biology and *Sinorhizobium* bacteria as a model object to design new agents that increase the resistance of crops to abiotic stress factors. This research area is critically important for boosting adaptive agricultural technologies and ensuring food security in a changing climate.

CONTRIBUTION

All the authors contributed equally to the study and bear equal responsibility for the information published in this article.

CONFLICT OF INTEREST

The authors declared no conflict of interest regarding the publication of this article.

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