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Review

Multipartite Interactions in the Soybean Rhizosphere: Unraveling the Molecular Mechanisms and Field Applications of Beneficial Microorganisms

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Abstract

Global food security requires sustainable increases in soybean production. However, excessive chemical fertilization imposes severe ecological limitations. This review maps the complex multipartite interactions in the soybean rhizosphere, integrating molecular advances, microbial consortia potential, and recent Brazilian regulatory frameworks. The analysis focuses on the synergistic benefits generated by symbiotic nitrogen-fixing bacteria (*Bradyrhizobium* spp.), associative plant growth-promoting rhizobacteria (*Bacillus* spp., *Pseudomonas* spp., and *Azospirillum* spp.), and arbuscular mycorrhizal fungi (AMF). These partners meet nitrogen demands, expand root architecture via phytohormones, and mine insoluble legacy phosphorus. Additionally, this integrated microbiome activates antioxidant defenses and induces systemic resistance against abiotic and biotic stresses. Institutionally, Law No. 15.070/2024 and Ordinance SDA/MAPA No. 1.270/2025 legally structure Brazil's bioinputs sector. Despite high agronomic potential, commercial establishment faces cell viability bottlenecks due to pesticide toxicity on seeds and biological contamination risks in on-farm production. The definitive consolidation of this technology depends on stable protective formulations and structured technical frameworks for analytical standardization and biosecurity in rural biofactories.

Keywords: arbuscular mycorrhizal fungi; bioinputs; *Bradyrhizobium*; legacy phosphorus; PGPR; regenerative agriculture

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1. Introduction

Global food security faces unprecedented challenges, with the world population projected to reach 9.7 to 10.4 billion by 2050 [1]. This demographic expansion and changing consumption habits pressure agricultural systems, driving an estimated 35% to 56% increased demand for high-quality protein [2,3] and up to 75% in global calories [4]. Paradoxically, chronic hunger persists amid an escalating scarcity of fertile land and water resources [5]. In this context, soybean (*Glycine max*) consolidates itself as the primary plant

protein source (~36% protein, 19% oil) [6]. Beyond direct human consumption, it underpins animal nutrition, comprising two-thirds of global protein meal production and ~30% of poultry feed [6]. Thus, these high-value grains constitute strategic tools for public health and global food security policies [7,8].

Reflecting this demand, the global soybean harvested area jumped from 23.82 million hectares in 1960 to 136.90 million in 2024, occupying ~6% of global arable land [9,10]. China drives international trade, importing ~105 million tons annually (85% of its domestic needs) primarily for industrial crushing to sustain its expanding livestock sector and meet vegetable oil demands [10]. This flow redirected the supply axis to South America, allowing Brazil to assume isolated global market leadership since 2012, currently supplying 50% to 55% of worldwide traded soybean [3]. Due to this centralization of supply, any significant South American yield failure could severely compromise global food security [9].

In Brazil, the soybean complex is a primary macroeconomic driver within an agribusiness sector that accounted for 25.13% of the 2025 Gross Domestic Product (GDP) [11]. This result, surpassing 2024's 22.9%, reflects the primary segment's expansion driving the agro-services sector [11]. The crop's hegemony is consolidated in national grain production (~50% of the volume), with harvests expanding from 171.48 to 180.13 million tons between the 2024/25 and 2025/26 cycles [12]. Geographically, Mato Grosso remains the main producing hub, concentrating ~29% of national output [12]. This high production is achieved within an optimized area, preserving most territory as native vegetation [3], which reinforces the need for biological efficiency technologies to mitigate horizontal agricultural expansion.

Within Brazilian public policies, this sustainability guideline is driven by the ABC Plan (2010–2020) for low-carbon agriculture [13] and currently ABC+ (2020–2030) [14]. Synergistically extending beyond the farm gate, soybean operates as the cornerstone of the national bioenergy matrix. Governed by the National Biodiesel Production and Use Program (PNPB) and the landmark "Combustível do Futuro" Law (No. 14.993/2024) [15], soybean oil supplies 65% to 70% of national biodiesel feedstock [16]. This regulatory framework mandates a progressive biofuel blending into fossil diesel up to 20% (B20) by 2030 [15], drastically curbing transport greenhouse gas (GHG) emissions and mitigating mineral diesel dependency [16], thus driving the transition toward cleaner energy sources.

Among field strategies incentivized by ABC+, Biological Nitrogen Fixation (BNF) stands out. Nitrogen is a primary limiting factor in tropical soils, and converting atmospheric N_2 into assimilable forms is restricted to specific microorganisms [13]. By mitigating GHG emissions, promoting carbon sequestration, and increasing fertility, these microbial bioinputs reduce operational costs and environmental risks [13], raising the systemic resilience of national agriculture [14].

Despite the historical role of synthetic fertilizers in agricultural productivity, their excessive and unbalanced use imposes severe ecological limitations [17,18]. Widely used nitrogen sources like urea face critically low use efficiency (30% to 40%) [19], with 40% to 70% lost via volatilization, leaching, or denitrification [20]. Surface application induces alkalization peaks that intensify ammonia (NH_3) volatilization by >50% [19], forming atmospheric particulate matter ($PM_{2.5}$) [18]. These deposits fuel acid rain, dissolving toxic free aluminum in soils [21]. Furthermore, ammonium (NH_4^+) oxidation via nitrification releases protons (H^+), accelerating soil acidification and generating a highly mobile nitrate (NO_3^-) surplus [22]. This residual NO_3^- infiltrates water bodies, triggering eutrophication and creating hypoxic/anoxic aquatic zones lethal to fauna [19,21]. Under anaerobic conditions, NO_3^- acts as an electron acceptor for denitrifiers, releasing nitrous oxide (N_2O), a potent GHG with a global warming potential ~300 times higher than carbon dioxide (CO_2) [18,22].

Analogously, massive inputs of chemical phosphate fertilizers face severe physicochemical restrictions, resulting in a real plant uptake rate of only 10% to 20% [23]. The remainder undergoes rapid sorption and stable precipitation with iron and aluminum in acidic soils, or calcium under alkaline conditions [24,25], accumulating as an insoluble inorganic liability [24]. Biologically, permanently elevated inorganic phosphate exerts feedback inhibition on native microbial phosphatases, blocking natural organic P cycling and worsening soil fertility decline [23]. Furthermore, continuous fertilization with processed marine sedimentary rocks acts as a chronic pathway for introducing bioaccumulative heavy metals (e.g., cadmium, chromium, lead, vanadium, zinc) into the soil–plant system [17,26]. Such sources can elevate soil cadmium by up to 49% [27], causing depressive phytophysiology triggered by oxidative stress [28]. This toxicity destroys cell membranes, inhibits root elongation, causes chlorosis, and drastically reduces crop biomass [27].

Facing the physicochemical collapse and ecological limitations of the intensive conventional model, contemporary agriculture must urgently reconcile yield increases with the adoption of biological matrices [29,30]. The depletion of the synthetic fertilizer route, marked by large-scale contamination, nutritional imbalance, and biodiversity loss, threatens agroecosystem stability [31,32]. This crisis establishes an urgent demand for sustainable, ecologically resilient plant nutrition management [33,34]. To break dependency on high-cost inputs and mitigate GHG emissions, strategies based on ecological intensification and bioaugmentation are imperative [35–37]. Consequently, agricultural science shifts toward exploiting soil biology, utilizing plant growth-promoting microorganisms and mycorrhizal fungi to restore the native microbiome [38,39]. These microbial consortia act as living tools capable of restoring biogeochemical balance, optimizing plant nutrition and defense without the collateral damage of chemical interventions [31,33,36].

This degradation requires an urgent transition toward ecologically integrated approaches [40]. Through "Green Agriculture", microbial bioinoculants consolidate as a highly biodegradable technological route, reversing the historical impacts of the Green Revolution [41–43]. Driven by the National Bioinputs Program and Law No. 15.070/2024 [44], the Brazilian bio-industry demonstrates strong maturity and sovereignty, with domestic capital accounting for 82.8% of registered commercial bioproducts by late 2024 [45]. This arrangement drives Circular Bioeconomy Systems (CBS), connecting organic waste reuse to large-scale biotechnological refining to mitigate risks in productive chains [46,47].

In the field, bioaugmentation focuses on optimizing nitrogen use efficiency and solubilizing complex minerals (P, K, Zn) to synchronize nutrient supply and mitigate N_2O emissions [48,49]. The inoculation of beneficial rhizobacteria, notably *Bradyrhizobium* spp. (establishing true symbiotic relationships) alongside *Azospirillum* spp., *Bacillus* spp., and *Pseudomonas* spp. (establishing associative, free-living dynamics), acts through synergistic pathways involving siderophores and regulatory phytohormones [50–52]. In weathered tropical soils, microbial and fungal-bacterial consortia containing *Trichoderma harzianum* reveal high synergism in root colonization and biomass accumulation [53,54]. In chickpea crops, a triple mixture (*Bradyrhizobium* + *Bacillus* + *Azospirillum*) expanded total dry mass by 62.6% [55], while multifunctional consortia in fruit trees validated reductions of up to 70% in chemical N and P inputs [56]. Regional meta-analyses endorse seed coating as the most efficient biological delivery method in these rhizospheric scenarios [54].

At the biotechnological vanguard, bioinput efficiency reaches the molecular level via extracellular membrane vesicles of Gram-negative bacteria, operating as type zero secretion systems (TOSS) for the protected trafficking of sRNAs, proteins, and metabolites [52,57]. This biochemical dialogue activates Induced Systemic Resistance (ISR), elicited by bacterial factors (flagella, LPS, volatile compounds) recognized by plant pattern receptors [51,58,59]. In parallel, Synthetic Biology (SynBio) and CRISPR-Cas9 editing allow the

design of inducible nitrogenase circuits in diazotrophs [49,60], enhanced by co-application with agricultural waste-derived humic and fulvic acids that regulate redox balance and induce core symbiotic genes like the *Rj4* gene [61,62]. However, biological fixation faces severe restrictions due to the high toxicity of traditional chemical seed treatments (e.g., carbendazim + thiram), which decimate inoculated beneficial populations [63]. To overcome these viability bottlenecks, bioresource engineering targets cellular encapsulation in polymeric matrices and in-furrow applications, demanding strong governance to support industrial scaling and regional bio-factories [64–67].

The consolidation of plant growth-promoting microorganisms requires robust regulatory governance to ensure bioproduct standardization. In Brazil, a significant milestone was the promulgation of Law No. 15.070/2024, establishing national guidelines for bioinputs [44]. To provide technical applicability, Ordinance SDA/MAPA No. 1.270/2025 formed a Working Group, including research institutes like Embrapa and sectoral entities like Aprosoja, to detail minimum parameters for bioinput registration [68]. This legal structuring mitigates market uncertainties and drives the large-scale adoption of microbial consortia.

Given the imperative need to systematically organize the vast scientific literature associated with regenerative agriculture, this review maps, synthesizes, and discusses the complex multipartite interactions in the soybean rhizosphere. Transitioning from the classical concept of tripartite symbiosis to an integrated microbiome perspective, we differentiate the true symbiotic relationships formed by biological nitrogen fixers (*Bradyrhizobium* spp.) and arbuscular mycorrhizal fungi (AMF) from the associative dynamics orchestrated by plant growth-promoting rhizobacteria (e.g., *Bacillus* spp., *Pseudomonas* spp., and *Azospirillum* spp.). To guide this comprehensive analysis, the present review is structured around the following highlight questions: (1) Molecular Mechanisms: How do the biochemical and genetic dialogues among rhizobia, AMF, and PGPRs synergistically modulate root architecture, biological nitrogen fixation, and legacy phosphorus mining? (2) Abiotic and Biotic Stress Mitigation: By what physiological pathways do these microbial consortia elicit systemic resistance and construct protective shields against edaphoclimatic constraints, such as drought, salinity, and heavy metal toxicity? (3) Field Application and Governance: What are the metabolic tradeoffs (C/N/P balance) associated with these interactions, and how can bioresource engineering and recent regulatory frameworks overcome viability bottlenecks to consolidate bioinoculants in large-scale agriculture?

2. The Diversity of Plant Growth-Promoting Microorganisms (PGPMs) in the Soybean Rhizosphere

2.1. Molecular and Physiological Mechanisms of Plant Growth Promotion

The establishment dynamics and structural diversity of the microbial community in the rhizosphere do not occur randomly; they are governed by a complex, bidirectional, and refined chemical signaling network originating in the root system of the host plant. Sugiyama [69] analytically details that the soybean crop acts actively and deliberately in the selection and recruitment of its own rhizospheric microbiome through targeted root exudation, releasing in a programmed manner specialized metabolites of high specificity, such as isoflavonoids and saponins. These chemical compounds transcend the basic function of energy supply, operating as true chemotactic signals that orchestrate the assembly and succession of the microbial community throughout the different phenological stages of the crop. In response to edaphoclimatic environmental pressures, the plant secretes selective compounds (including flavonoids, citrates, and amino acids) through efflux systems controlled by specialized transporter proteins belonging to the ATP-Binding Cassette (ABC) and Multidrug and Toxic Compound Extrusion (MATE) families. This chemical input

functions as a modulation trigger in the rhizosphere, to which plant growth-promoting rhizobacteria (PGPR) respond by finely adjusting the expression of their own membrane transporters, optimizing the colonization rate and efficiency of functional interactions [70] (Figure 1A).

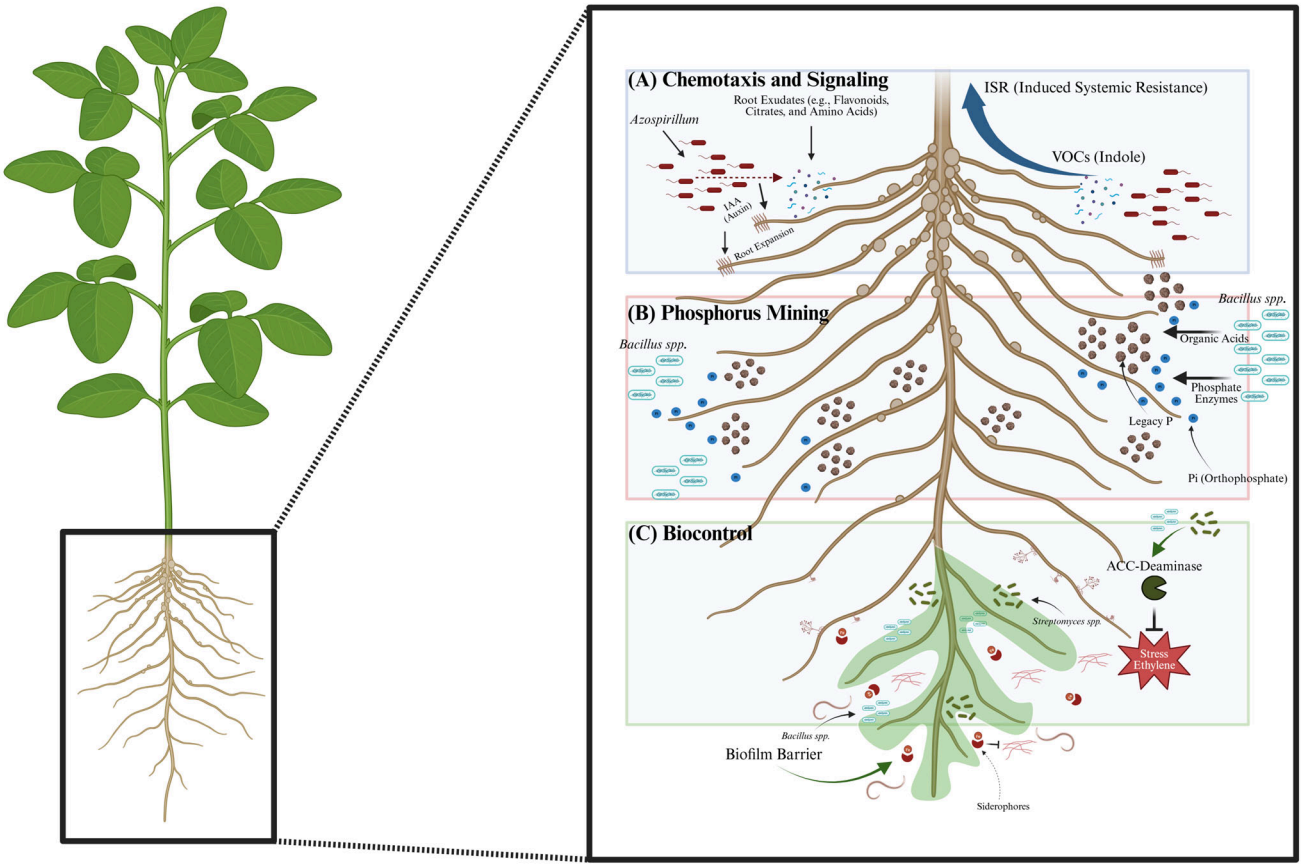

Figure 1. Multifunctional direct and indirect plant growth-promoting pathways orchestrated by rhizobacterial consortia (PGPR) in the soybean rhizosphere. The comprehensive integration of bacterial mechanisms is divided across three distinct functional layers: (**A**) Chemotaxis and Signaling: Host roots programmatically release selective exometabolites (e.g., flavonoids, citrates, and amino acids) to actively recruit beneficial diazotrophs, such as *Azospirillum*. Bacterial secretion of indole-3-acetic acid (IAA) drives lateral root expansion, while long-distance airborne signaling mediated by volatile organic compounds (VOCs), such as indole, primes Induced Systemic Resistance (ISR) in distal tissues. (**B**) Phosphorus Mining: Elite PGPR strains (*Bacillus* spp.) exude short-chain organic acids and phosphate-solubilizing enzymes to alter soil adsorption constants, effectively solubilizing insoluble legacy phosphorus (Legacy P) into bioavailable orthophosphate (Pi) for plant uptake. (**C**) Biocontrol and Stress Mitigation: Rhizospheric colonization by *Bacillus* spp. and *Streptomyces* spp. establishes a protective physical biofilm barrier. Concurrently, high-affinity bacterial siderophores sequester free iron (Fe) from the soil matrix, inducing nutritional deprivation that efficiently suppresses soil-borne oomycetes and pathogenic nematodes. To alleviate abiotic constraints, bacterial 1-aminocyclopropane-1-carboxylate (ACC) deaminase cleaves root ethylene precursors, suppressing stress ethylene accumulation to preserve root homeostasis. Abbreviations: ACC, 1-aminocyclopropane-1-carboxylate; Fe, iron; IAA, indole-3-acetic acid; ISR, induced systemic resistance; PGPR, plant growth-promoting rhizobacteria; Pi, inorganic orthophosphate; VOCs, volatile organic compounds. (Created in BioRender. Paraginski, J. A. (2026) https://BioRender.com/pj2advx).

Additionally, the biological signaling mediated by these rhizobacteria expands beyond the immediate physical limits of the underground environment, reaching distal tissues through the emission of Volatile Organic Compounds (VOCs). A striking example of this

phenomenon is indole, an active metabolite secreted by rhizobacteria such as *Proteus vulgaris* JBLS202, whose airborne stimulus functions as a long-distance signaling molecule [71] (see VOCs in Figure 1A). This gaseous compound directly interferes with complex hormonal pathways of the host plant, triggering a precise biochemical interplay and crosstalk involving the combined regulation and signaling of auxins, cytokinins, and brassinosteroids, demonstrating that the microbial communication network coordinates vegetative vigor systemically [72].

Following successful recruitment, PGPRs stimulate plant development through direct mechanisms of action, which essentially involve active facilitation in the acquisition of limiting nutritional resources in strict consonance with the host's exogenous phytohormonal modulation [73–75]. Within the scope of hormonal phytostimulation and plant structural alteration, the genus *Azospirillum* stands out historically as the most widely employed and validated bacterial inoculant in the global agricultural scenario [75]. The official Brazilian recommendation for the co-inoculation of *Bradyrhizobium* spp. with the elite strains Ab-V5 and Ab-V6 of *A. brasilense* is based on the strict biological and synergistic complementarity of these genera [76]. The significant morphological gains derived from this integrated management are mostly attributed to the improvement of the three-dimensional architecture and geometric expansion of the root system through the direct action of bacterial phytohormones, with emphasis on auxins. Elite strains of the genus, such as HM053, demonstrate a significantly higher indole-3-acetic acid (IAA) biosynthesis capacity when compared to standard commercial strains [77,78]. This continuous hormonal input acts directly as a mitotic and cell differentiation trigger for the development of lateral roots and root hairs, expanding the total surface area of the absorptive system. This morphological increase substantially elevates the absorptive capacity of water and mineral nutrients, promoting documented average increments of up to 16.8% in forage production [76], and acts indirectly by optimizing infection success and maximizing the sites available for subsequent nodulation by *Bradyrhizobium* strains [77,78].

The magnitude of these morphological responses is strictly mediated by edaphoclimatic factors and cropping systems, notably the No-Tillage System (NTS). While the structural stabilization of soil matrices under NTS preserves a favorable microenvironment for bacterial persistence [79], the lack of plant species diversity in continuous short-interval crop successions (such as soybean–maize) acts as a restrictive biological filter, often depressing the overall soil bacterial diversity [80,81]. Under these simplified succession regimes, targeted bioaugmentation through the application of multifunctional rhizobacterial consortia, such as the combined application of *Pseudomonas chlororaphis* H1 and *Bacillus altitudinis* Y1 [82], or *Bacillus subtilis* and *Paraburkholderia sabiae* [83], becomes an indispensable intervention to artificially replenish the rhizosphere, restoring core biochemical functionalities and safeguarding plant nutritional homeostases [84–86].

By geometrically expanding the root network, the plant prepares the ideal structure for Biological Nitrogen Fixation (BNF). This biochemical process, by which N_2 is reduced to NH_3 by diazotrophic bacteria (notably of the genus *Bradyrhizobium*) through catalysis promoted by the nitrogenase enzyme complex, plays a fundamental role in the sustainability of soybean cultivation. It supplies the massive N input required for the biosynthesis of proteins, acting to meet an average metabolic balance of 80 kg of N for every 1000 kg of grains produced [87,88]. In the Brazilian scenario, based on the pioneering research of Dr. Johanna Döbereiner [89–91], the continuous selection of highly efficient genotypes strictly adapted to tropical soils transformed this technology into a strategic macroeconomic pillar, reaching an adoption rate of about 85% of the country's total production area and generating estimated annual savings between 15 and 20 billion dollars [88,92–97] (Table 1).

Table 1. Physiological mechanisms and quantitative agronomic responses for plant growth promotion, symbiotic establishment, and stress mitigation by diazotrophic bacteria and PGPR consortia reported in the literature.

Treatment/ Consortium	Crop/Condition & Environmental Stress	Physiological & Molecular Mechanism	Quantifiable Agronomic Response	References
Azospirillum brasilense HM053	Soybean; early root colonization	Higher indole-3-acetic acid (IAA) biosynthesis acts as a mitotic trigger for lateral roots and indirectly optimizes infection success, maximizing the sites available for subsequent nodulation by *Bradyrhizobium*.	Elevates the absorptive capacity of water and mineral nutrients, promoting significant morphological gains in the root system.	[77,78]
Bradyrhizobium + *Azospirillum brasilense* + *Rhizophagus intraradices*	Soybean; soil waterlogging stress (hypoxia)	Temporarily compensates for the reduction in BNF through the maintenance of alternative nitrogen fluxes and protective enzymatic regulation.	Maintains significantly higher levels of amino acids and ureides under stress, allowing a much faster metabolic recovery post-hypoxia.	[98]
Bradyrhizobium + *Bacillus* + *Azospirillum* (Triple mixture)	Chickpea; field trials	Synergistic integration of multiple functional pathways and shared rhizospheric colonization.	Expanded shoot dry mass by 62.2% and total dry mass by 62.6%.	[55]
Bradyrhizobium diazoefficiens + *Rhizobium tropici* (CIAT 899)	Common bean; open field conditions	Involvement of complementary systemic phytohormonal stimulation and favorable modifications in the root network.	Results in yield increases of up to 20% under real field conditions when compared to single inoculation with *R. tropici*.	[99,100]
Bradyrhizobium japonicum + *Azospirillum brasilense* + foliar Co and Mo	Soybean; open field management	Mo acts as an indispensable catalytic cofactor for nitrogenase complex regulation; Co acts in cobalamin (vitamin B12) synthesis required for leghemoglobin to regulate oxygen flux inside the nodules.	Significantly increases the number of pods per plant and the 100-grain weight, resulting in average yield increases of up to 10%.	[90,101–103]
Bradyrhizobium japonicum USDA 110 + *Pseudomonas putida* NUU8	Soybean; severe water restriction/drought	Secretion of 1-aminocyclopropane-1-carboxylate (ACC) deaminase cleaves the ethylene precursor in the root, preventing the abortion of symbiotic nodules under water scarcity.	Raises the number of nodules by 17%; significantly improves mineral nutrient uptake and protective soil enzymatic activity.	[104–106]
Bradyrhizobium spp. (Elite strains)	Soybean; characteristically deficient tropical soils	Catalysis promoted by the nitrogenase enzyme complex to convert atmospheric N_2 into plant-assimilable forms.	Reaches an adoption rate of about 85% of the production area; generates estimated annual macroeconomic savings between 15 and 20 billion dollars.	[87,88,93]
Bradyrhizobium spp. + *Azospirillum brasilense* (Ab-V5, Ab-V6)	Soybean; high-performance managed fields	Complementation of functional mechanisms: nitrogen fixation coupled with the active bacterial secretion of phytohormones.	Provides stable yield gains ranging between 4% and 25%; consistently maximizes crop yield to support high-performance harvests exceeding 6000 kg ha^{-1}.	[76,77,107, 108]

Abbreviations: ACC, 1-aminocyclopropane-1-carboxylate; BNF, biological nitrogen fixation; Co, cobalt; IAA, indole-3-acetic acid; Mo, molybdenum; N_2, atmospheric nitrogen; USDA, United States Department of Agriculture.

Advanced genomic research reveals that the evolutionary adaptation of elite strains and natural variants of *Bradyrhizobium japonicum* and *B. diazoefficiens* to restrictive ecosystems is governed by complex structural modifications incorporated into their symbiotic islands. These variants present single nucleotide polymorphisms (SNPs) and indels in essential genes involved in nitrogenase biosynthesis and maturation, specifically *nifE* and *nifS*, as well as the metabolic gene *coaE* and LysR-type transcriptional regulators, conferring crucial competitive advantages [94,109]. However, the efficiency of symbiosis is a highly genetically regulated process, depending on strict reciprocal molecular recognition. This checkpoint is mediated by specific genetic loci, such as *GmNNL1*, which encodes a resistance (R) protein capable of interacting directly with the NopP effector of *Bradyrhizobium* strains. This specific interaction triggers an immune response that inhibits infection via root hairs, restricting symbiotic compatibility and limiting nodule numbers, an endogenous control mechanism reflecting the complexity of coevolution [110] (the GmNNL1–NopP checkpoint is schematized in Figure 2).

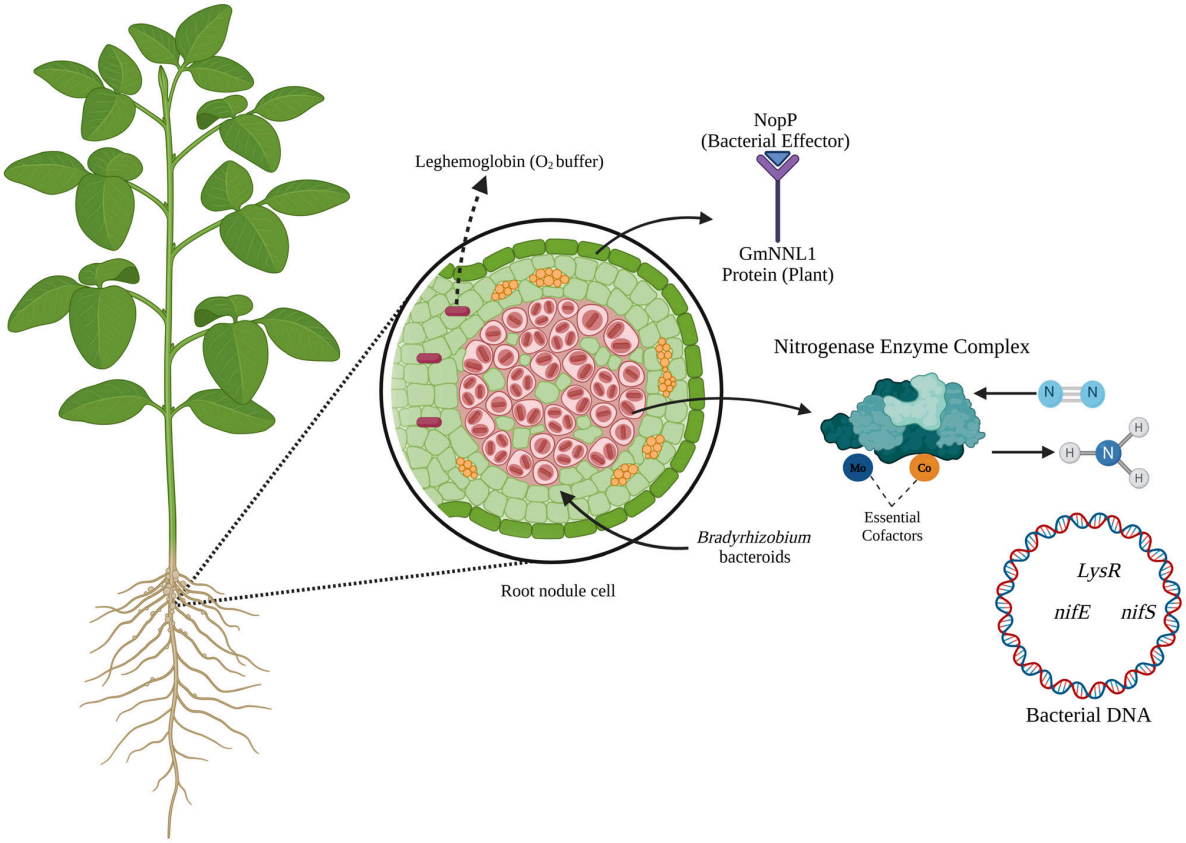

Figure 2. Molecular checkpoints, genomic infrastructure, and symbiotic mechanisms of biological nitrogen fixation (BNF) in the soybean rhizosphere. A detailed macro-to-micro schematic highlighting the genetic and physiological dialogue established during the *Bradyrhizobium* symbiosis. At the cell interface, the specific compatibility checkpoint is governed by the direct molecular binding of the plant resistance receptor protein (GmNNL1) to the bacterial outer protein effector (NopP) to autoregulate root infection and nodule numbers. Within the root nodule cell, elite strains and natural variants display crucial evolutionary adaptations driven by single nucleotide polymorphisms (SNP_S) and indels in core genes (*nifE*, *nifS*) structurally managed by the *LysR* transcriptional regulator family. Intracellular oxygen flux is strictly buffered by a functional leghemoglobin matrix to shield the oxygen-sensitive nitrogenase enzyme complex. The nitrogen fixation process ($N_2 \rightarrow NH_3$) is sustained by Molybdenum (Mo), acting as an indispensable structural catalytic cofactor, and Cobalt (Co). Abbreviations: BNF, biological nitrogen fixation; Co, cobalt; Mo, molybdenum; N_2, atmospheric nitrogen; NH_3, ammonia; NopP, nodulation outer protein P. (Created in BioRender. Paraginski, J. A. (2026) https://BioRender.com/4n29r15).

The understanding of rhizospheric biochemical reactions elucidates that this fixing efficiency is strongly synergistic when associated with the planned supply of essential mineral micronutrients, specifically cobalt (Co) and molybdenum (Mo). Mo acts as an indispensable catalytic cofactor for the structural regulation of the nitrogenase complex, while Co acts directly in the synthesis of cobalamin (vitamin B12), a molecule required for leghemoglobin to regulate oxygen flux inside the nodules [101] (Figure 2). Experimental field data confirm that co-inoculation of *B. japonicum* and *A. brasilense*, associated with leaf supply of Co and Mo, significantly increases the number of pods per plant and the 100-grain weight, resulting in average yield increases of up to 10% [78,102,103]. The integration between synthetic fertilizers and the symbiotic system requires rigorous calibration; strategic applications of small nitrogen doses at crop startup ("N-starter" at ~30 kg N ha^{-1}) optimize yield components without inhibiting nodulation, whereas high doses (60 kg ha^{-1}) tend to compromise molecular signaling [111]. To optimize these agronomic benefits, there is an imperative need to select genetic materials with high biological compatibility, considering the genetic background and level of promiscuity of cultivars [112]. Faced with the need to maximize yield ceilings, the paradigm of co-inoculation combined with PGPRs consistently outperforms single inoculation, proving indispensable for achieving high-performance harvests exceeding 6000 kg ha^{-1} [107,108,113]. This success is expanded by dual inoculation with *Glomus fasciculatum* in alluvial soils [114], integration with *Pseudomonas* isolates [115], and advanced tripartite microbial augmentation combining *Bradyrhizobium*, *Bacillus*, and the endophytic fungus *Piriformospora indica* to enhance the overall nutrient profile [116,117]. This synergism extends to other legumes, where triple mixtures (*Bradyrhizobium* + *Bacillus* + *Azospirillum*) in chickpea expanded total dry mass by 62.6% [55], and co-inoculation of *B. diazoefficiens* with *Rhizobium tropici* in common bean resulted in yield increases of up to 20% under real field conditions [99,100] (these agronomic responses are summarized in Table 1). Furthermore, the efficiency and stability of BNF are intrinsically linked to plant mineral nutrition, with emphasis on phosphorus (P) availability, whose deficiency severely limits nodulation and overall symbiotic performance [118,119]. Limited P availability restricts mycorrhizal colonization, preventing it from exerting its full growth-promoting effect; however, the expression of phosphate transporters of the *PHT1* family in roots and nodules is specifically altered by the symbiosis, showing that the plant triggers a reprogramming of its orthophosphate acquisition pathways in response to chronic deficiency [118]. Therefore, the strategic application of mineral phosphorus, when coordinated with bacterial inoculation, maximizes nodulation and sustains the high bioenergetic demand during nodule development [119].

Beyond nitrogen acquisition, the planned introduction of specific microbial groups emerges as a high-performance biotechnology to overcome the economic bottlenecks associated with "Legacy Phosphorus" (legacy P). Pavinato et al. [120] demonstrated that an alarming fraction of the P applied via soluble mineral fertilizers undergoes rapid reactions of fixation and chemical adsorption on soil iron and aluminum oxides, accumulating in highly stable and insoluble forms. The strategic introduction of phosphate-solubilizing bacteria (PSB) functions as an efficient tool for "mining" this legacy P by altering the equilibrium constants of the soil adsorption–desorption matrix through the continuous exudation of short-chain organic acids and the catalytic activity of phosphatase enzymes [121]. Elite strains such as *Bacillus megaterium* (CNPMS B119) and *Bacillus subtilis* (CNPMS B2084) express complementary multifunctional mechanisms of P solubilization and mineralization through the coordinated production of specific phytase enzymes and high chemical affinity siderophores [122–124] (see Phosphorus Mining in Figure 1B).

In parallel, arbuscular mycorrhizal fungi (AMF) establish an ancestral mutualistic association that acts as a high-precision biological regulator for this nutritional interface [76,125].

Extending their hyphae and extraradical mycelia into the rhizosphere, AMFs significantly expand the absorptive surface area and overcome nutrient depletion zones, which is vital in tropical soils [76,126]. Temporal dynamics show that viable spore density in the soil is prominent pre-planting, whereas internal root colonization and differentiation of functional exchange structures (arbuscules and vesicles) reach their maximum activity peaks in the maturation and reproductive stages, dominantly occupied by morphotypes of the genera *Glomus*, *Acaulospora*, *Gigaspora*, and *Diversispora* [125,127].

Because AMFs do not possess autonomous saprophytic capacity to directly hydrolyze complex organic soil compounds, they rely on a cooperative association with PSB to mine legacy P [128]. In this interactive tripartite mechanism, continuous exudation of fructose by the extraradical fungal mycelium serves as an assimilable carbon source that stimulates the metabolic activity of PSB in the mycorrhizosphere. In response, bacterial populations activate the secretion of phosphomonoesterase and phytase enzymes, cleaving insoluble organic fractions into free orthophosphate (Pi), which is subsequently captured by fungal hyphae through specific molecular transporters and translocated directly to the host [128–130] (refer to the Root Cortical Cell microenvironment in Figure 3). This synergism, when orchestrated with diazotrophic bacteria, enhances the biological responses of the legume in a manner superior to single isolated infections, generating significant increases in total dry mass and accumulated nitrogen [131].

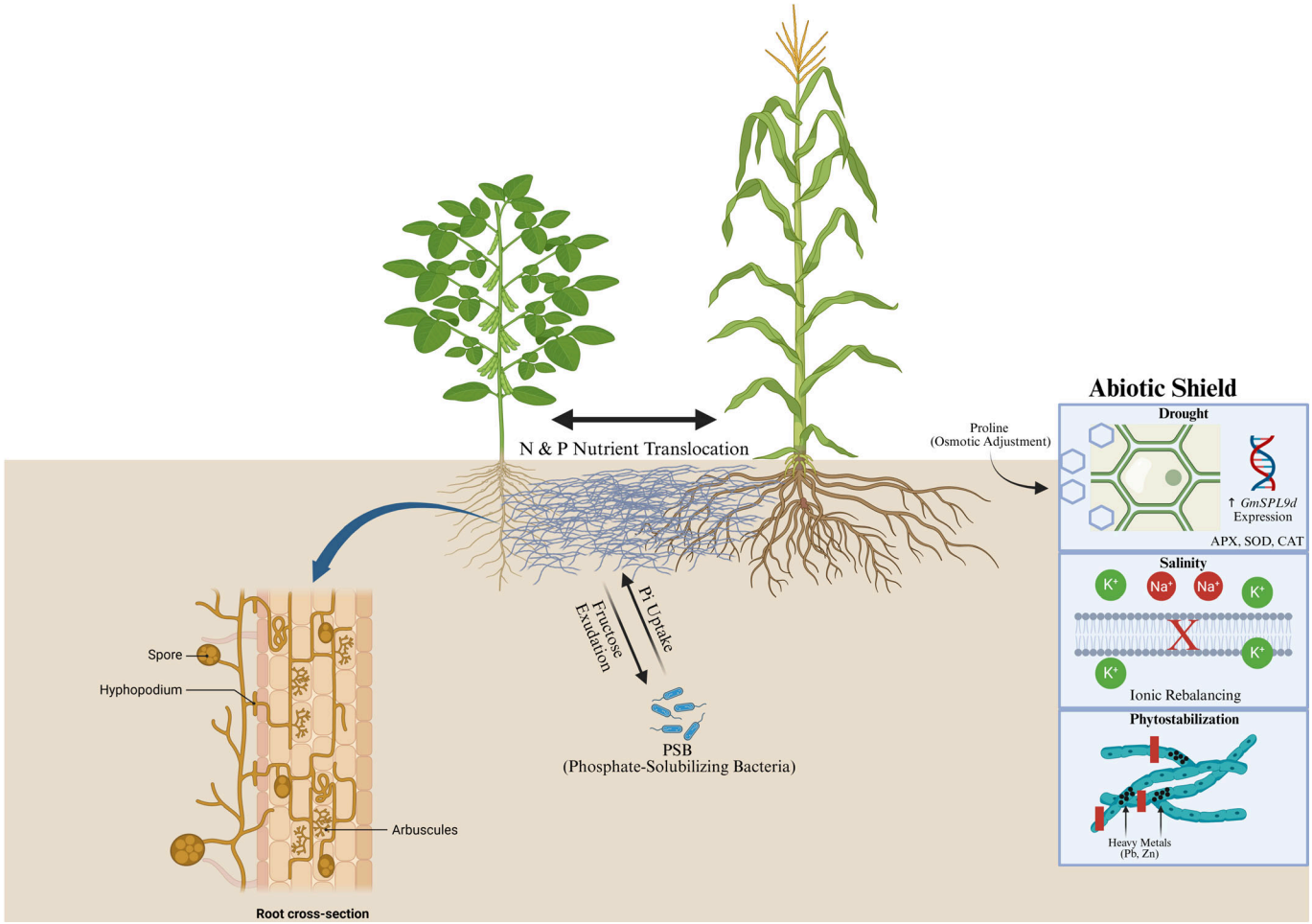

Figure 3. Ecological integration of arbuscular mycorrhizal fungi (AMF) in common mycorrhizal networks (CMNs) and multidimensional physiological shields against environmental and ecotoxic stresses. An underground ecological overview showcases a CMN establishing continuous physical links between intercropped soybean and maize systems to govern interspecific nutrient (N & P) translocation

based on source-sink dynamics. The magnified root cross-section details the fungal anatomy (spores, hyphopodium, and arbuscules) and highlights a synergistic interactive interface where fungal fructose exudation serves as a carbon source that stimulates phosphate-solubilizing bacteria (PSB) to release orthophosphate (Pi) for subsequent fungal uptake. The multi-tiered Abiotic Shield panels illustrate protective mechanisms: (Drought) osmotic adjustment via proline accumulation and *Gm-SPL9d* overexpression to up-regulate cellular APX, SOD, and CAT antioxidant enzymes; (Salinity) maintenance of ionic rebalancing through K^+ accumulation and Na^+ exclusion; and (Phytostabilization) a biological filtration barrier where mycorrhizal fungi compartmentalize hazardous heavy metals, such as Lead (Pb) and Zinc (Zn), within the underground matrix, actively restricting their toxic translocation to the shoots. Abbreviations: APX, ascorbate peroxidase; CAT, catalase; CMN, common mycorrhizal network; K^+, potassium; N, nitrogen; Na^+, sodium; P, phosphorus; Pb, lead; Pi, inorganic orthophosphate; PSB, phosphate-solubilizing bacteria; SOD, superoxide dismutase; Zn, zinc. (Created in BioRender. Paraginski, J. A. (2026) https://BioRender.com/miinocq).

The ecological and nutritional implications of these fungal networks expand markedly when analyzed from the perspective of Common Mycorrhizal Networks (CMNs) in intercropping systems. CMNs establish continuous underground physical connections that interconnect root systems of neighboring plants, facilitating interspecific transfer and redistribution of nutrients based on source-sink dynamics [132,133]. In upland rice-soybean intercropping, the legume acts as the dominant species in direct P acquisition through fine plastic modifications in its root morphology, while rice demonstrates a strict dependence on mycorrhizal colonization, highlighting a crucial functional complementarity [134]. Similarly, in soybean–maize intercropping systems, dual inoculation facilitates the uptake and direct transfer of N from soybean to maize through connected hyphae [135] (as illustrated by the CMN in Figure 3). This biological potential can be further intensified through integrated management, such as the combined application of AMF with biochar-based structured fertilizers, which reconfigures nutritional acquisition pathways and promotes biomass increases of up to 19.45% [136], consolidating the broad regulatory potential of these multipartite interactions in large-scale biological nutrient cycling.

2.2. The Biotic and Abiotic Shield: Systemic Resistance and Edaphoclimatic Tolerance

In parallel to morphological alterations, PGPRs coordinate the activation of complex systemic defense networks in the plant against biotic stresses and pathogens, operating through well-delineated molecular pathways. Fukami et al. [137] elucidate that the Induced Systemic Resistance (ISR) triggered by these PGPRs in the host plant is finely coordinated by the jasmonic acid and ethylene signaling pathways in a manner strictly independent of the salicylic acid pathway. This molecular behavior differs fundamentally from Systemic Acquired Resistance (SAR), which is classically dependent on regulated levels of salicylic acid, although both immune processes converge and require the mediation of the multigenic regulatory protein NPR1 for their phenotypic expression. This plant immunization model corroborates the classic conclusions of De Vleesschauwer et al. [138], confirming that beneficial microorganisms promote the *priming* phenomenon of host cellular defenses, enabling distal and foliar tissues for a substantially faster and more vigorous immune response against subsequent attacks, without incurring the severe metabolic costs or energy trade-offs commonly associated with active pathogenic infections. This indirect protective stimulus is reinforced by the action of active substances generated in the rhizosphere, where bacteria continuously stimulate the jasmonate and ethylene pathways, reducing susceptibility to pests in distant aboveground tissues [74,139,140]. Additionally, PGPRs utilize direct mechanisms of exclusion and antibiosis in the rhizospheric environment, notably the synthesis of potent antibiotics and the massive production of siderophores, high-affinity iron-chelating molecules that sequester free iron in the soil, suppressing the growth

of phytopathogenic fungi and oomycetes through nutritional deprivation [74,141,142] (see Biocontrol in Figure 1C).

Regarding biotic stress, the bacterial diversity established in the rhizosphere exerts a markedly suppressive effect against phytopathogens and underground pests through multiple simultaneous mechanisms of biological control and antibiosis. Experimental inoculation with *Streptomyces* strains (mainly SS14 and IT20) elucidates that the targeted modulation of the rhizospheric bacteriome, characterized by the recruitment and induction of secondary beneficial genera such as *Devosia* and *Pseudomonas*, is fundamental for the suppression of aggressive oomycete pathogens, such as *Phytophthora capsici*, constituting a sustainable alternative to the use of synthetic chemical pesticides [143]. In the biological control of soil fungal diseases and oomycetes, the study by León et al. [144] describes the selection of *Pseudomonas fluorescens* and *Bacillus amyloliquefaciens* strains (with emphasis on the BNM340 strain) endowed with potent antifungal action against *Pythium ultimum* in soybean, demonstrating that aggressive root colonization associated with the production of siderophores, hydrolytic enzymes, and surfactant antimicrobial lipopeptides (such as surfactin and iturin A) is crucial to suppress pathogens and ensure seedling emergence and initial stand [144,145].

Furthermore, the sustainability of the symbiotic system strictly depends on root health, which can be vulnerable to severe biotic stresses. Integration of cultural management strategies, such as the use of cover crops in succession, proves to be a highly effective practice to confer soil suppressiveness. The biological control of aggressive endopathogenic phytonematodes, such as *Meloidogyne incognita* and *Pratylenchus brachyurus*, through the synergistic association between cover crops and specific biocontrol agents, proves to be a determining factor in protecting the anatomical integrity of the root system and ensuring the full nodulation and infection potential of *Bradyrhizobium*, enabling a more effective bacterial colonization and protecting BNF stability under conditions of strong pathogen pressure [146]. Integrated management involves the control of phytonematodes that severely challenge soybean sustainability in tropical ecosystems such as the "Cerrado" bioma. Oliveira et al. [147] demonstrated the efficacy of biological control of the root-lesion nematode (*Pratylenchus brachyurus*) in soybean using consortia with *Trichoderma asperellum* and *Trichoderma harzianum*. These beneficial agents exert antibiosis and active suppression through the synthesis and release of peroxidases and hydrolytic enzymes, such as chitinase and β-1,3-glucanase, capable of directly degrading the pathogen's cuticle, a plant defense mechanism supported by the investigations of van Loon et al. [148] and Vinale et al. [149]. The validation of this protective response in commercial cultivars such as BRSGO Caiapônia and BRS 8560RR highlights the technical viability of these strains in maintaining the crop's productive potential under strong biotic pressure [150]. Within the specific scope of the biocontrol of severe underground pests, selected strains of the genus *Bacillus* exhibit a potent and documented direct nematicidal effect aimed at the suppression of the soybean cyst nematode (*Heterodera glycines*). As reported in detail by Zhou et al. [151], the application of elite strains such as *Bacillus aryabhattai* (Ba1–7) and *Bacillus megaterium* (Ba2–4 and Ba2–6) demonstrated high efficacy under real field conditions, focused on the drastic reduction in the infective female population of *H. glycines* and the consequent increase in total seed number produced per plant. The strain Ba2–6, specifically, stood out for its high biocontrol capacity, reaching a rate of 93.85% mortality of second-stage juveniles (J2) of the nematode, validating the biotechnological importance of *Bacillus* spp. as efficient biological substitutes for traditional synthetic nematicides and pesticides [151] (Figure 1C). This functional versatility confers a prominent position to the genus *Bacillus*, consolidating its application in both growth promotion and integrated biological control. Vasques et al. [152] highlight the relevance of this multifunctional application in the Brazilian agricultural

scenario, demonstrating how these bacteria modulate adaptive physiological responses and confer robust phytosanitary protection through the sustainable production of bioactive compounds [153].

Regarding the mitigation of edaphoclimatic abiotic stresses, co-inoculation and the strategic use of microbial consortia associated with organic conditioners emerge as high-performance pathways to safeguard the physiological integrity of the crop. Water deficit resulting from drought constitutes one of the main bottlenecks for crop sustainability, since it compromises active mineral absorption and the total N content accumulated in plant tissues [104]. Under such restrictive conditions, the synergy promoted by the inoculation of *B. japonicum* USDA 110 acts in a providential manner in the plant, expanding root length by up to 56% and increasing root dry biomass by 47%, mechanically shielding the nodulation process and ensuring stable yield increments in the face of water scarcity [104] (Table 2). Under restrictive scenarios of severe water deficit, Silva et al. [154] report that the joint application of *B. japonicum* and *A. brasilense* under critical drought conditions (equivalent to only 25% of field capacity) resulted in significant increases in root volume and root dry mass of soybean. This adaptive success is based on the continuous production of IAA, which stimulates cell elongation and root hair proliferation, geometrically expanding the plant's capacity to explore and absorb water in deep soil layers [154]. Furthermore, bacterial indole-3-acetic acid (IAA) acts as a master regulator of agricultural adaptive resilience; it not only expands root cell walls but also broadens root exudation, creating a crucial signaling feedback loop to recruit and attract additional beneficial bacterial communities to the rhizosphere under hostile environments [152]. Similarly, in cowpea cultivation, Fontes et al. [155] confirmed that the joint application of *B. japonicum* and *A. brasilense* significantly enhances total nitrogen content while stimulating foliar defensive flavonoids. This tripartite synergism is supported by the multiple mechanisms of action model proposed by Bashan and de-Bashan [156]. This symbiotic and morphological resilience can be significantly amplified through the integration of PGPRs with humic substances (HS) or organic biostimulants, which act directly as modulating agents of the expression of stress-response genes, improving ionic homeostasis and minimizing the negative impacts resulting from water scarcity [157]. In parallel, the joint application of potassium humate and PGPRs in degraded soils effectively preserves the stability of soybean cell membranes, minimizing oxidative stress damage through the elevation of endogenous antioxidant enzyme levels, including catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) [158].

Table 2. Protective mechanisms and quantitative agronomic responses of microbial consortia against abiotic and biotic stresses in the soybean rhizosphere.

Treatment/ Consortium	Crop/Condition & Environmental Stress	Physiological & Molecular Mechanism	Quantifiable Agronomic Response	References
Bradyrhizobium japonicum USDA 110	Soybean; restrictive water deficit scenarios/drought	Mechanical shielding of the nodulation process and preservation of baseline active mineral absorption	Expands root length by up to 56% and increases root dry biomass by 47%	[104]
Bradyrhizobium japonicum USDA 110 + *Pseudomonas putida* NUU8	Soybean; severe water restriction/drought	Exacerbation of protective rhizosphere enzymes; monosaccharides, organic acids, and flavonoids from root exudates act as molecular signaling triggers	Raises the number of nodules by 17%; significantly improves mineral nutrient uptake and protective soil enzymatic activity	[105,106]

Table 2. *Cont.*

Treatment/ Consortium	Crop/Condition & Environmental Stress	Physiological & Molecular Mechanism	Quantifiable Agronomic Response	References
Guided application of PGPR	Soybean; high salinity environments	Metagenomic restructuring of microbial diversity; optimization of carbon assimilation and starch synthesis via sucrose synthase and fructokinase; up-regulation of cellular APX, GR, and MDHAR	Substantial increase of 32.57% in the final grain yield; efficiently protects the photosynthetic apparatus against oxidative damage	[159]
Bacillus aryabhattai (Ba1–7) or *Bacillus megaterium* (Ba2–4 and Ba2–6)	Soybean; severe underground pest pressure	Direct nematicidal effect and targeted biological suppression via sustainable synthesis of bioactive compounds	Reaches a rate of 93.85% mortality of second-stage juveniles (J2) of *Heterodera glycines* via the strain Ba2–6; drastic reduction in infective females	[151]

Abbreviations: APX, ascorbate peroxidase; GR, glutathione reductase; MDHAR, monodehydroascorbate reductase; PGPR, plant growth-promoting rhizobacteria.

At the molecular level, the metabolic reprogramming promoted by PGPR under severe water deficit involves profound modifications in the metabolism of lipids and structural proteins. Sheteiwy et al. [160] showed that inoculation with *Bacillus amyloliquefaciens* induces a marked up-regulation of the *GmPK* and *GmBCCP2* genes, keys for lipid biosynthesis and membrane stabilization, as well as the *GmGy1* and *GmGy2* genes, intimately associated with the synthesis of storage and stress proteins, whereas genes linked to cell degradation and senescence pathways, such as *GmACX1* and *GmCysP1*, are strongly repressed. Furthermore, the application of this PGPR results in greater intracellular accumulation of ATP and in the vigorous activation of membrane ATPases, such as H^+-ATPase, Ca^{2+}-ATPase, and Mg^{2+}-ATPase, providing the electrochemical gradient necessary to govern the active transport of metabolites and ions, a fundamental mechanism to ensure the maintenance of cell turgor, osmotic stability, and the continuity of growth under water restriction [160]. Under the same drought scenario, the co-inoculation of *B. japonicum* USDA110 with *Pseudomonas putida* NUU8 acts synergistically on crop resilience. Jabborova et al. [104] demonstrated that this bacterial consortium induces a significant enrichment in the activity of key soil enzymes, including proteases and acid and alkaline phosphomonoesterases, which catalyze the hydrolysis of complex organic compounds into readily bioavailable amino acids and soluble phosphates. This integrated response is chemically stimulated by the specific composition of soybean root exudates (such as monosaccharides, organic acids, and flavonoids), which act as essential molecular signals in chemotaxis and structural modeling of the microbial community in the mycorrhizosphere [105]. Additionally, the capacity of these PGPRs to secrete the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase acts by cleaving the direct precursor of ethylene in the root, minimizing the physiological stress of the host and preventing the inhibition of root growth and the abortion of symbiotic nodules under water scarcity [105].

The performance of *Bradyrhizobium* strains under severe water deficit is substantially optimized through the establishment of tripartite microbial consortia involving arbuscular mycorrhizal fungi (AMF). As verified by Nader et al. [161], inoculation of *B. japonicum* in consortium with AMF confers robust protection to soybean against the stress induced by irrigation suppression at the critical R3 and R5 stages, promoting significant increases in

active nodules number, final nitrogen content in seeds, and agronomic yield compared to the uninoculated control. This synergistic microbial interaction acts by adjusting plant metabolism to ensure that nodulation is not aborted during water scarcity, maintaining productivity at satisfactory levels and validating the functions of these biological fixers in arid and semi-arid environments [161–163]. Additionally, co-inoculation with AMF (such as *Gigaspora rosea* and *Rhizophagus clarus*) in different soybean varieties favors the combined uptake of N and P, attenuating the deleterious effects of water stress through the increase in synthesis of key antioxidant enzymes and stimulating the cellular accumulation of protective compatible solutes, preserving the integrity of nitrogen fixation processes, quality, and final yield [150,164]. Under severe water stress scenarios, mycorrhizal symbiosis acts as an indispensable homeostatic buffer for plant survival and physiological maintenance. Inoculation with *Rhizophagus clarus* in soybean cultivars (such as Anta82 and Desafio) subjected to prolonged drought periods allowed a superior maintenance of stomatal conductance and photosynthetic efficiency, preventing premature senescence through the active modulation of cellular water homeostasis [136]. This adaptive morphophysiological response is corroborated by Soliman et al. [165], who demonstrated that under severe water restriction (equivalent to 25% of field capacity), AMF colonization induces a marked up-regulation of genes involved in polyamine biosynthesis, promoting significant improvements in photosynthetic parameters and stomatal conductance. Mechanistically, symbiosis established by species of the genera *Glomus* and *Gigaspora* alters the host's overall physiological metabolism, promoting protective osmotic adjustment through the targeted accumulation of compatible solutes, such as proline and soluble sugars, in addition to robustly activating antioxidant enzymatic systems responsible for scavenging reactive oxygen species, conferring drought tolerance [166].

At the molecular and biotechnological level, overexpression of the *GmSPL9d* gene in transgenic soybean lines acts synergistically with the fungus *Rhizophagus irregularis* under water deficit, resulting in a superior antioxidant regulation capacity via ascorbate peroxidase (APX), superoxide dismutase (SOD), and catalase (CAT), shielding the photosynthetic apparatus against degradation induced by water scarcity [132,167] (see Drought mechanisms in Figure 3). Additionally, protective impacts of mycorrhization extend to the preservation of industrial and nutritional quality components of seeds under stress. As reported by Machiani et al. [168] and Lotfabadi et al. [169], inoculation with *Funneliformis mosseae* and other AMFs in soybean under water restriction significantly improves the grain lipid profile, elevating the concentration of essential unsaturated fatty acids (oleic and linoleic) and activating key antioxidant enzymes (APX, SOD, GPX) that mitigate cellular senescence processes. This metabolic stabilization is ratified by Zirak-Qoturbulagh et al. [150], who highlight that AMF inoculation drastically reduces cellular oxidative damage and improves fundamental morphological and biochemical parameters for yield. By integrating mycorrhizal colonization with *Bradyrhizobium* activity, the plant manages to maintain physiological homeostasis even under severe water stress conditions, validating the use of these stable symbiotic consortia as indispensable tools to mitigate climate change effects in rainfed agriculture [150].

The bioenergetic basis of this drought tolerance relies on the capacity of AMFs to physically and chemically expand the so-called enzymatic hotspots in the rhizosphere. Mycorrhizal inoculation positively alters glucose exudation by root apices, expanding the area of these high biogeochemical activity zones by up to 53% under drought conditions [170–172]. This readily available carbon input serves as an energy source for the associated microbiota of the mycorrhizosphere, reducing substrate turnover and keeping microbial functionality active [172,173]. Biochemical and molecular analyses demonstrate that the tripartite consortium between AMF (*Glomus* spp. isolates) and *Bradyrhizobium*

substantially elevates the activity of enzymes such as β-glucosidase and dehydrogenase in rhizospheric soil, accelerating P mobilization from native organic sources [174,175]. This complex structured microbiome creates a highly active rhizospheric environment capable of sustaining cellular metabolism and mitotic division of the host, monitored via cell cycle regulation by flow cytometry, under severe water restrictions that would paralyze uninoculated plants [160,175]. This dynamic can be significantly enhanced and restructured through integrated management practices involving the use of biochar. As demonstrated by Liu et al. [176], integration of biochar with inorganic and organic fertilizers in purple soils profoundly alters the rhizospheric microbial community, stimulating the relative abundance of beneficial fungi and actinobacteria, which translates into yield increases of up to 96.7%. Evaluating the direct interaction between biochar and AMF under water stress, Jabborova et al. [106] found a striking structural improvement in soybean roots, observable by a bulky increase in root volume, projected area, and root diameter, responses accompanied by a surge in mycorrhizal spore density and rhizospheric activity of alkaline phosphomonoesterase and dehydrogenase enzymes. In turn, BNF becomes highly vulnerable under soil waterlogging stress conditions (hypoxia), which causes severe metabolic disorganization in the nodules due to a drastic reduction in oxygen diffusion, directly inhibiting the catalytic activity of the nitrogenase complex. This waterlogging stress induces a significant decrease in the activities of the enzymes glutamine synthetase (GS) and NADH-glutamate synthase (NADH-GOGAT), which are fundamental for the assimilation pathways of the ammonium generated in the fixation process [138,139]. However, the strategic co-inoculation of *Bradyrhizobium* with *A. brasilense* and the mycorrhizal fungus *Rhizophagus intraradices* acts by efficiently mitigating these deleterious effects; plants subjected to this integrated management maintain significantly higher levels of amino acids and ureides under stress, suggesting that the multipartite association temporarily compensates for the reduction in BNF through the maintenance of alternative nitrogen fluxes and protective enzymatic regulation, allowing a much faster metabolic recovery of the plant after the soil reoxygenation period [98].

Salinity stress and extreme thermal fluctuations represent other severe challenges to plant homeostasis that find efficient responses in rhizospheric microbial dynamics. Soybean yield and sustainability depend directly on the adaptive efficiency of integrated biological inputs in the rhizosphere, where the development of protective strategies and the planned use of biofertilizers based on local microorganisms emerge as the most viable alternatives to mitigate damage, maintain plant homeostasis, and safeguard the morphological and physiological responses of the crop against severe environmental variations [101]. Regarding salinity, the action of specific halotolerant bacteria, such as *Pseudomonas koreensis* MU2, enhances efficiency in silicon and phosphorus utilization, mitigating the deleterious effects of salt stress by promoting ionic rebalancing (a positive balance in K^+ accumulation and reduction of Na^+) coupled with the coordinated activation of cellular antioxidant systems [177] (see Salinity mechanisms in Figure 3). The understanding of specific isolates and their genetic mutations directly determines the efficiency of this phytostimulation in salinized soils. As demonstrated by El-Esawi et al. [178], the *Bacillus firmus* SW5 strain robustly attenuates salt toxicity in soybean by reconfiguring the root network, promoting nutrient acquisition, and modulating the expression of genes encoding antioxidant enzymes (ascorbate peroxidase—APX, catalase—CAT, peroxidase—POD, and iron superoxide dismutase—Fe-SOD) and key salinity tolerance genes (*GmVSP*, *GmPHD2*, *GmbZIP62*, *GmWRKY54*, *GmOLPb*, and *CHS*), controlling the oxidative stress caused by the accumulation of hydrogen peroxide and malondialdehyde (MDA). On the other hand, the determinants of bacterial survival also regulate this success: Costa-Gutierrez et al. [179] reported that, although *Pseudomonas putida* KT2440 increases seedling vigor under salinity,

specific mutations in the *eptA* gene disrupt the synthesis of lipopolysaccharides (LPS) and exopolysaccharides (EPS) of the bacterial outer membrane, which severely compromises its survival and competitive fitness in the rhizosphere, reducing inoculation efficiency. Metagenomic mappings conducted by Lin et al. [159] observed that the guided application of PGPR under salt stress positively restructured soil microbial diversity, promoting the enrichment of beneficial bacterial phyla such as Bacteroidetes, Firmicutes, and Nitrospirae, in addition to the entomopathogenic and helper fungal genus *Metarhizium*. This rearrangement in the rhizospheric community optimized carbon assimilation and starch synthesis in the plant through the coordinated activation of key metabolic enzymes, such as sucrose synthase and fructokinase. Simultaneously, the microbial treatment elevated the activity of plant antioxidant system enzymes, including ascorbate peroxidase (APX), glutathione reductase (GR), and monodehydroascorbate reductase (MDHAR), efficiently protecting the photosynthetic apparatus against oxidative damage caused by reactive oxygen species, which culminated in a substantial increase of 32.57% in the final grain yield under high salinity [159] (see Table 2 for a summary of PGPR agronomic and protective outputs).

When faced with the deleterious effects of saline and saline-alkaline stress, mycorrhizal symbiosis acts as a physiological and molecular reprogramming system for the host. Under elevated salinity levels (e.g., 200 mM NaCl), the establishment of the symbiosis undergoes severe biological restrictions, with a drastic inhibition in the fungal colonization rate and in development of arbuscules and vesicles, affecting sensitive soybean genotypes in a substantially more severe manner than tolerant ones [180]. Characteristically acidified soils represent another severe ecological challenge. Under such conditions, symbiosis with adapted species, such as *Glomus deserticola*, directly assists in buffering the rhizospheric pH, preserving the host's metabolic performance [181]. However, the active presence of AMF inocula, such as *Funneliformis mosseae* and *Rhizophagus intraradices*, reconfigures the plant's defense systems against oxidative damage to membranes, attenuating cellular stress by significantly reducing the levels of hydrogen peroxide (H_2O_2), thiobarbituric acid reactive substances (TBARS), and malondialdehyde (MDA) [180,182]. This metabolic rebalancing under high salinity is ensured by the increase in endogenous phytohormonal levels of auxins, including IAA and indole-3-butyric acid (IBA), coupled with the rigorous preservation of the content of photosynthetic and photoprotective pigments (chlorophylls a, b, and carotenoids), preserving cellular vigor [180]. Furthermore, under saline-alkaline stress, Peng et al. [183] demonstrated that inoculation with a multi-species AMF consortium (*Funneliformis mosseae*, *Rhizophagus intraradices*, and *Diversispora epigaea*) promotes a 23.11% increase in the soil available P content, efficiently integrating fungal uptake pathways with the host's root strategy to sustain productivity. Pu et al. [184] complement this scenario by showing that salt stress induces plastic modifications in root morphology that are differentially modulated by the presence of native AMFs or by the introduction of exogenous AMFs. The magnitude of this adaptive potential reaches an exceptional level when mycorrhizal symbiosis is integrated with the specific supplementation of key micronutrients. Cun et al. [101] recorded an unprecedented synergistic effect when associating fungal species of the genus *Glomus* (*G. intraradices*, *G. constrictum*, and *G. microcarpum*) with the application of 0.6% molybdenum (Mo) under severe salt stress in soybean. This integrated management resulted in drastic improvements in the crop's morphophysiological parameters, including increases of 65.91% in plant height, 67.01% in stomatal conductance, 18.45% in chlorophyll SPAD value, and 22.15% in root dry weight, associated with a 48.67% expansion in root system length. Supported by robust methodological and analytical references and by the observations of Cruz-Paredes et al. [185], the study by Cun et al. [101] revealed that the co-factorization of Mo with AMF significantly elevates the biochemical activity of salt-affected soil, inducing increases in catalase (85.17%), urease (53.19%), and dehydrogenase

(56.21%) activities (these multilinear physiological and soil chemical reconfigurations are compiled in Table 3). This joint fertilization directly mitigates the P deficiency resulting from salt restriction, simultaneously promoting an 84.85% surge in spore density and raising mycorrhizal colonization intensity (M%) to 27.63%, consolidating the efficacy of this integrated biological complex. Additionally, under the thermal stress scenario, Kang et al. [186] identified and characterized the promising strain *Bacillus tequilensis* SSB07, which exhibits the singular capacity to synthesize an integrated set of gibberellins (GA1, GA3, GA5, GA8, GA19, GA24, and GA53), as well as IAA and abscisic acid (ABA). Inoculation with *B. tequilensis* SSB07 induced an efficient thermotolerance in soybean plants, resulting in increases in biomass and chlorophyll content under high-temperature stress through the endogenous and systemic modulation of jasmonic acid and salicylic acid levels in the phyllosphere. As reviewed by Keswani et al. [187], the elucidation of microbial biosynthesis of gibberellins and other secondary hormones represents a rapidly expanding field in soil science, offering robust technological alternatives to mitigate plant vulnerability and gradually reduce dependency on industrial chemical fertilizers.

Table 3. Ecosystem interactions, chemical changes, and multidimensional agronomic benefits of Arbuscular Mycorrhizal Fungi (AMF) symbioses reported in the literature.

Treatment/ Consortium	Crop/Condition & Environmental Stress	Physiological & Molecular Mechanism	Quantifiable Agronomic Response	Reference
AMF + Biochar-based structured fertilizers (BF)	Soybean; sustainable crop rotation systems	Reconfiguration of nutrient acquisition pathways; reduces energy dependence on direct rhizobial nodulation in favor of mycorrhizal paths	Promotes increases of up to 19.45% in biomass and grain yield	[136]
Biochar + inorganic and organic fertilizers	Soybean; purple soil profiles	Bulky restructuring of the soil microbial complex, altering physical and microbiological traits to accelerate nutrient cycling	Translates into crop yield increases of up to 96.7%	[176]
Multi-species AMF consortium (*Funneliformis mosseae*, *Rhizophagus intraradices*, *Diversispora epigaea*)	Soybean; saline-alkaline soil restrictions	Efficient integration of fungal uptake pathways with the host's root morphological strategy to sustain productivity	Promotes a 23.11% increase in the soil available phosphorus (P) content	[183]
Glomus isolates (*G. intraradices*, *G. constrictum*, *G. microcarpum*) + 0.6% Molybdenum (Mo)	Soybean; under severe salt stress conditions	Acceleration of soil biochemical activity; drives a massive 84.85% surge in spore density and raises internal colonization intensity (M%) to 27.63%	Increases plant height by 65.91%, stomatal conductance by 67.01%, chlorophyll SPAD value by 18.45%, root dry weight by 22.15%, and root system length by 48.67%; induces sharp increases in catalase (85.17%), urease (53.19%), and dehydrogenase (56.21%) soil activities	[76]

Beyond water and osmotic restrictions, the tripartite cooperation established among roots, rhizobia, and AMFs constitutes a decisive biochemical and cellular protective barrier

for overcoming heavy metal and soil contaminant toxicities. In soils characterized by low P availability and severe lead (Pb) contamination, symbiosis with *Rhizophagus intraradices* acts as a highly efficient phytostabilization and biological filtration strategy, retaining toxic metal ions in a compartmentalized manner within root tissues and facilitating the selective translocation of P to the shoots, which preserves the integrity of the photosynthetic machinery and sustains soybean productivity in the face of ecotoxic stress [188,189]. Likewise, inoculation with *Rhizophagus irregularis* regulates the expression of specific metal stress-response genes, confining heavy contaminants to the underground system and preventing their deleterious translocation to the aboveground vegetative and reproductive organs [167]. In the face of stress caused by excess and toxicity of zinc (Zn) in the soil, Ibiang et al. [190] recorded that dual inoculation with *Gigaspora rosea* and *Bradyrhizobium diazoefficiens* successfully restores soybean ionic homeostasis through the systemic and coordinated balancing of iron (Fe) and manganese (Mn) translocation from the roots to the shoot tissues. This fine nutritional modulation controls the structural integrity of cell membranes and robustly attenuates damages derived from lipid peroxidation, drastically reducing early defoliation rates and elevating total crop dry biomass, empirically validating the theses of mutualistic synergism and multipartite functional complementarity advocated by Antunes et al. [191] and Chalk et al. [192] (Figure 3).

2.3. Metabolic Trade-Offs and C/N/P Stoichiometry Under Climate Change

The establishment of multipartite interactions is not metabolically free; rather, it imposes a substantial energetic toll on the host plant. To assemble and maintain a beneficial rhizosphere microbiome, plants allocate up to 20% of their photosynthetically fixed carbon and 15% of their assimilated nitrogen exclusively toward root exudation [70,193,194]. This massive metabolic flux is actively governed by complex transporter networks (such as SWEETs for sugar export, and ABC, MATE, or ALMT families for secondary metabolites and organic acids) which continuously drain resources from the root to sustain the microbial community [70]. Interestingly, this carbon sink is not uniform; exudation follows strict spatial patterns along the root axis (e.g., root tips versus mature zones) to optimize microbial colonization precisely where it is most needed for active nutrient acquisition [70,195,196].

Within the specific context of nodulation and mycorrhization, the fungal and bacterial partners act as secondary carbon sinks, driving intense metabolic competition in the rhizosphere [70,197]. Because sustaining microbial metabolism with photosynthetically fixed carbon is energetically expensive, plants must strictly balance stoichiometric C/N/P trade-offs [198,199]. Longitudinal studies and metabolomic analyses (GC-MS) confirm that this resource allocation is highly dynamic. Bulky application of soluble mineral fertilizers (above 20–40 kg P_2O_5 ha^{-1}) markedly inhibits the AMF root colonization rate [200]. In such high fertility scenarios, modern soybean genotypes register significant reductions in endogenous levels of isoflavonoids (such as genistein and daidzein) in response to mycorrhization, highlighting the metabolic cost imposed when the carbon drain to the fungus overrides the nutritional benefits [201]. Conversely, genotypes endowed with greater symbiotic affinity reprogram this metabolism to optimize phosphorus use efficiency under moderate restriction [201,202]. To prevent the squandering of precious carbon reserves on redundant or inefficient microbial engagements, legumes have evolved sophisticated "nutrient checkpoints" that closely monitor internal nitrogen (N) and phosphorus (P) status before committing to symbiosis [199]. The GRAS-type transcription factors Nodulation Signaling Pathway 1 (NSP1) and NSP2 are central to this regulatory hub, linking the plant's nutritional needs to the biosynthesis of critical rhizospheric signals, such as strigolactones and flavonoids [199,203].

A recent breakthrough in understanding this metabolic reprogramming is the identification of the NSP2-MYB40 regulatory module, which serves as a paradigm for stoichiometric control in legume interactions [199]. Under conditions of severe N and P starvation, NSP2 physically interacts with MYB40, a nodulation-induced transcription factor [199]. This heteromeric complex directly targets and strongly activates the promoters of flavonoid biosynthetic genes, notably chalcone O-methyltransferase 1 (*ChOMT1*), leading to the localized accumulation of specific signaling molecules like isoliquiritigenin and 4,4′-dihydroxy-2′-methoxychalcone (DHMC) in the root epidermis [199]. By stringently restricting the costly biosynthesis of these flavonoids to periods of actual nutrient limitation, the plant fine-tunes its interaction efficiency and dynamically optimizes nitrogen acquisition without exhausting its basal carbon budget [199].

In the context of global climate change, where abiotic stresses and variable soil fertility constantly shift metabolic demands, this tightly orchestrated stoichiometric balance becomes a vital survival strategy. If the continuous carbon cost required to maintain nodules and the mycorrhizal network surpasses the nutritional benefits gained, the plant can rapidly adjust its exudation profile by modulating these transcription factors and transporter families [70]. Understanding the cross-talk between localized nutrient checkpoints (like NSP2-MYB40) and systemic regulatory pathways, such as C-terminally encoded peptides (CEPs) that signal global nitrogen status is fundamental [199,204] (Figure 4). Unlocking these mechanisms is crucial to leveraging synthetic microbial communities in the field without imposing detrimental carbon drainage and yield penalties on the crop.

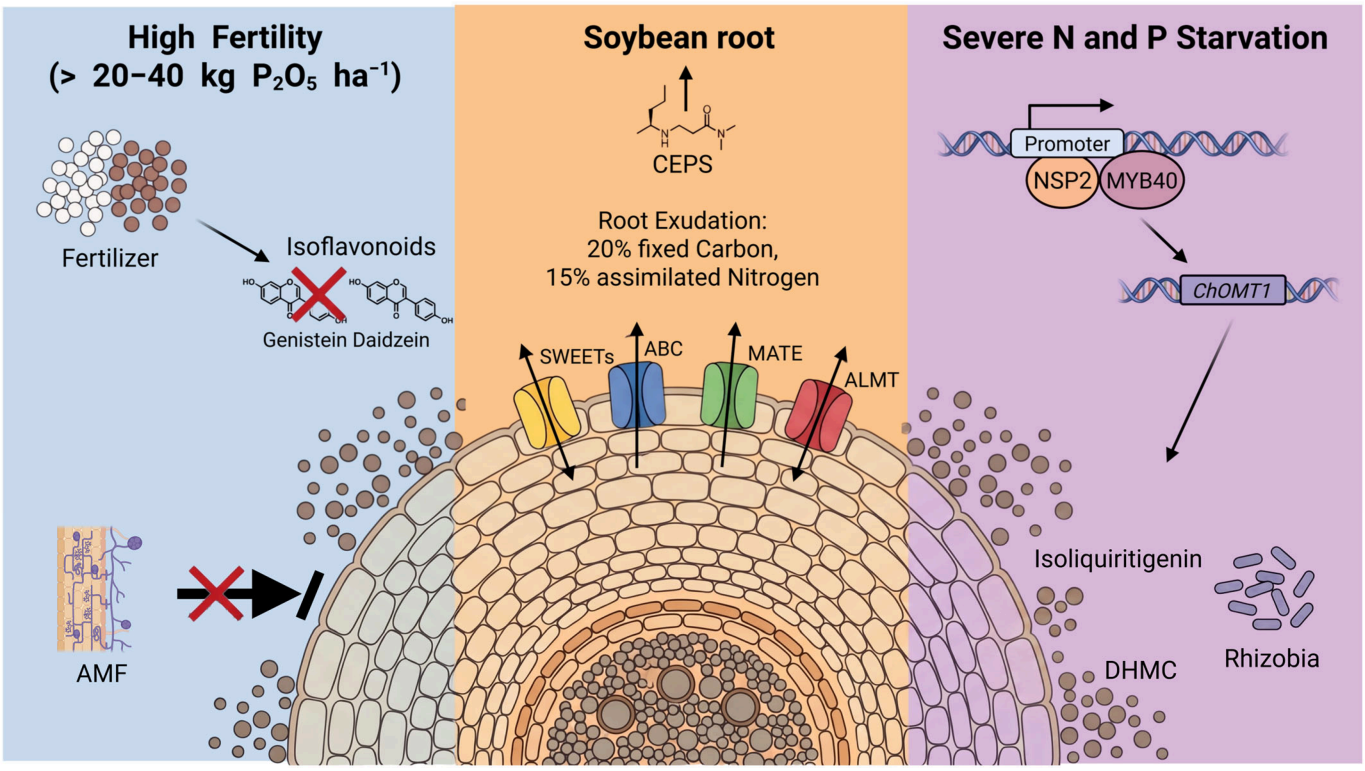

Figure 4. Metabolic trade-offs and stoichiometric regulation in the soybean rhizosphere under contrasting nutritional scenarios. (Center) The host plant allocates up to 20% of fixed carbon and 15% of assimilated nitrogen exclusively toward root exudation. This continuous resource drain is governed by complex transporter networks (SWEETs, ABC, MATE, and ALMT) that export metabolites outward into the soil. Concurrently, systemic nitrogen status is signaled to the shoot by C-terminally encoded peptides (CEPs). (Left) Under high fertility scenarios (>20–40 kg P_2O_5 ha^{-1}), the plant mitigates metabolic costs by significantly reducing the endogenous levels of isoflavonoids (such as genistein and daidzein) and markedly inhibiting the root colonization rate by arbuscular mycorrhizal fungi (AMF).

(Right) Under severe N and P starvation, the NSP2-MYB40 regulatory module physically interacts to activate the *ChOMT1* promoter. This genetic activation triggers the localized accumulation of specific signaling molecules (isoliquiritigenin and DHMC) in the root epidermis, dynamically optimizing rhizobial symbiosis without exhausting the basal carbon budget. (Created in BioRender. Paraginski, J. A. (2026) https://BioRender.com/jpkwmiv).

2.4. Field Applications, Viability Bottlenecks, and Agronomic Efficacy

From a broad geographical perspective, field studies conducted in diverse edaphoclimatic environments in the USA revealed that, in soils with a previous history of continuous soybean cultivation and in the absence of severe abiotic stresses, the adoption of additional inoculation strategies, whether through supplemental seed coating or via late soil application in the early vegetative or reproductive stages, did not promote significant increases in grain yield or changes in seed protein composition when strictly compared to the conventional inoculation practice performed at planting time [205]. However, the large-scale expansion of soybean fields and the consequent compression of the sowing operational window have imposed new and complex logistical challenges on soybean growers, demanding biotechnological advances focused on making field management more flexible. According to Hungria et al. [96], the development of technologically advanced liquid formulations containing specific cellular protectors has enabled the practice of seed pre-inoculation up to 15 days prior to sowing. This advance allowed overcoming the historical barrier of drastic bacterial viability loss commonly observed in traditional early treatments, detailed by Deaker et al. [206] and Herridge [207]. Ensuring the efficacy of this biotechnological management requires rigorous analytical control on the seed. Santos et al. [208] emphasize that *Bradyrhizobium* survival on the seed is a critical factor, warning that methodologies for the recovery and counting of viable cells, previously validated and standardized for soybean, are not directly transposable to other seed species without specific methodological adjustments in extraction techniques and diluents used, running the risk of masking and underestimating the actual concentration of viable cells of the inoculant prior to planting.

To efficiently transfer this biological potential from experimental scales to the large-scale market, the development of appropriate formulation and application technologies for microbial inoculants is indispensable. The choice of carrier substrate is a critical factor, directly determining the adherence capacity of fungal and bacterial propagules to the seed surface and the subsequent initial colonization rate of roots. Carriers based on stable matrices of vermiculite or peat exert distinct influences on the viability and protection of the inoculum, and calibrating these physical properties is a mandatory step to ensure the reproducibility of the technology on a commercial scale [209]. Additionally, the incorporation of mycorrhizal and bacterial inocula via seed coating techniques or priming methodologies has consolidated as a highly effective pathway to ensure early microbial survival. This technological management promotes more uniform germination, elevates initial seedling vigor, and accelerates hyphal establishment in the soil profile, conferring fundamental adaptive advantages under sowing scenarios in challenging environments [210]. Moreover, the use of multifunctional microorganisms constitutes a technology fully consolidated within the regulatory framework of bioinputs for the physiological conditioning of seeds, allowing a vigorous initial establishment under challenging field conditions [211].

Ultimately, the long-term efficiency and consistency of the biological response in low-chemical-input agriculture depend on the biological specificity between the colonizing agents and the plant genotype, as well as on the management guidelines adopted in the production system [212]. Wang et al. [213] analytically demonstrated that post-colonization growth responses in soybean are highly variable, transitioning from markedly beneficial effects to scenarios of agronomic indifference depending strictly on the fungal isolate and

host genotype used, showing that this adaptive variability is not necessarily linked to the intrinsic phosphorus acquisition efficiency of each genetic material. Complementarily, land-use history and crop rotations exert a decisive biological filter in the rhizosphere. The previous and continuous cultivation of non-mycorrhizal species, such as canola (*Brassica napus*), induces a negative legacy effect (primarily driven by the release of suppressive root exudates, including glucosinolate-derived isothiocyanates, among others) that severely depresses the AMF colonization rate in the subsequent soybean crop, requiring rigorous analytical monitoring of edaphic microbial dynamics to safeguard symbiotic effectiveness [214]. Conversely, sustainable agricultural systems integrating long-term no-tillage and agroforestry arrangements sustain a significantly higher mycorrhizal spore richness compared to intensive monocultures, converting the rhizosphere into a biologically more resilient environment [215]. Likewise, continuous monoculture practices versus diversified rotation systems structurally alter microbial biodiversity, indirectly impacting the protein quality and proximate composition of fatty acids in soybean seeds, where targeted inoculation tends to optimize the overall protein content of the grains [216].

Finally, the plant itself exerts a strong selection pressure on microbial communities transitioning from the rhizospheric soil to the root endosphere. Zhang et al. [217] observed that the alpha diversity of AMF communities in soybean is highly sensitive to soil fertilization levels, demonstrating that mineral nitrogen input induces significant variations in the relative abundance of dominant taxonomic groups, such as the genus *Glomus* (family Glomeraceae), and highlighting the existence of a selective filter exerted by the plant that must be carefully considered when planning large-scale commercial inoculations. To circumvent these limitations, Rossetim et al. [218] validate the feasibility of introducing complex functional microbial consortia integrating AMFs, PGPRs, and bioactive metabolites of *Trichoderma*, promoting robust yield increments and consolidating integrated microbiome management as a key strategy for the sustainable development and nutritional enhancement of the crop under the frontiers of modern mineral nutrition established by Marschner [219] and Marra et al. [220].

The successful transition of these biotechnologies from a strictly laboratory scale to large-scale incorporation into commercial agriculture has redesigned the institutional, regulatory, and operational structures of the productive sector in South America. As outlined by Medina et al. [145], a continuous and strategic effort is observed in countries like Argentina and Brazil to validate and establish robust commercial products based on PGPRs and microbial consortia, placing these biological agents at the vanguard of regional agribusiness. However, for this vanguard to consolidate on a large scale, the institutional scenario faces complex challenges inherent to the transition from an agricultural regime historically centered on chemical pesticides and fertilizers to a paradigm based on sustainable bioinputs. The development and effective technology transfer of these tools require well-delineated sectoral strategies, with an emphasis on the need for the regionalization of production, aiming to adapt microorganisms to local edaphoclimatic specificities, and on the creation of specific, agile, and unbureaucratic regulatory frameworks [221].

In the sociotechnical analysis developed by Goulet [222], the normative and market advancement verified in Brazil promoted an unprecedented integrative alignment between the niche of ecological alternatives and the traditional agroindustrial regime. In the Brazilian normative context, this emerging technological and industrial ecosystem is guided by structuring state decisions. Decree No. 10.375 [223], and its subsequent amendment by Decree No. 11.940 [224], established the National Bioinputs Program (PNB) and its Strategic Council under the coordination of the Ministry of Agriculture and Livestock (MAPA), regulating products, processes, and technologies of microbial, plant, or animal origin to boost the sustainable bioeconomy. This institutional structuring is corroborated

by the need for biological inputs to be understood and regulated as high-value strategic goods, originating from rigorous biotechnological processes that involve controlled stages from primary production in biofactories to post-harvest storage parameters, aiming at the replacement of synthetic chemical inputs [225]. The socioeconomic and environmental relevance of this transition from chemical inputs to biological matrices is validated by the strategic study conducted by MAPA and the Inter-American Institute for Cooperation on Agriculture (IICA) [226], which estimates that expanding the use of biological inoculants in major grain crops is capable of generating an annual savings of up to US$ 5.1 billion for Brazilian agribusiness, in addition to mitigating greenhouse gas emissions by up to 18.5 million tons of carbon equivalent. From the standpoint of global sustainability, Tufail et al. [18] emphasize that the large-scale transition to biological matrices and bioinputs is an essential guideline to mitigate the severe impacts of environmental pollution and greenhouse gas emissions generated by the soybean production chain, consolidating microbial biotechnology as an essential pillar for a sustainable future [18,226,227].

The Brazilian Bioinputs Program acts by decisively promoting the decentralization of biological production [228]. This scenario of strong institutional stimulus has driven the decentralized proliferation of rural "biofactories" aimed at the multiplication of microorganisms on agricultural properties themselves (on-farm production), bringing operational field practices closer to the "do-it-yourself biology" movement, as characterized by Goulet et al. [229]. However, this rapid territorial extension generated intense controversies between the academic community of microbiology and official research bodies. Specialists warn that biological multiplication processes conducted in a rural area environment without rigorous control of asepsis, sterilization, and isolation present serious risks of biological contamination and accidental dissemination of mutant or opportunistic pathogenic agents to the environment and public health. This overview highlights the critical and contemporary challenge of establishing structured technical frameworks that ensure the correct laboratorization, biosecurity monitoring, and strict analytical standardization of these rural facilities to protect the agronomic efficacy of the bioinputs [229].

3. Final Considerations and Future Perspectives

The paradigm shift from intensive conventional agriculture to a regenerative and ecologically integrated model, anchored in the principles of Green Agriculture and the Circular Economy, consolidates soybean microbiome management as an irreversible and highly strategic technological pathway. The strategic rationalization of chemical matrices through the targeted integration of microbial bioinputs not only mitigates severe environmental externalities (such as low urea efficiency, nitrate leaching, nitrous oxide emissions, and heavy metal accumulation via continuous phosphate fertilization) but also restores the vigor and resilience of agroecosystems in the face of global climate challenges. Crucially, while external phosphorus (P) applications remain fundamentally necessary to compensate for crop grain removal and to satisfy the high chemical fixing capacity of weathered tropical soils, bioaugmentation shifts the focus toward mining the stable soil legacy P liability, thereby reducing the structural reliance on massive, highly soluble mineral inputs.

The integrated analysis of literature confirms that yield ceiling and stability of contemporary soybean cultivation are optimized when the agronomic approach shifts from isolated strains to the use of multifunctional microbial consortia and multipartite interactions (*Bradyrhizobium* + PGPR + AMF). This rhizospheric synergism operates through multiple complementary biological mechanisms: the genus *Bradyrhizobium* supplies the crop's high nitrogen demand, while the genus *Azospirillum* and other PGPRs expand the root architecture three-dimensionally via phytohormone secretion, broadening infection sites and the plant's absorptive capacity. Concurrently, the introduction of phosphate-

solubilizing bacteria (such as *Bacillus* and *Pseudomonas*) acts in mobilizing the legacy phosphorus accumulated in the soil, a process enhanced by the extraradical mycelium networks of arbuscular mycorrhizal fungi, which overcome depletion zones and translocate free orthophosphate directly to the host. Under water, saline, or biotic stresses, this integrated microbiome activates key antioxidant enzymatic systems, induces systemic resistance, and confers root phytosanitary protection against pathogens and phytonematodes.

Despite advances at the molecular vanguard, including signal trafficking via extracellular vesicles and activity circuits controlled by synthetic biology tools, the field application of these biological matrices runs into practical bottlenecks of cellular viability. Low compatibility of traditional chemical pesticide mixtures applied to seeds remains a persistent challenge, steering bioresource engineering toward encapsulation in polymeric matrices and driving the large-scale adoption of in-furrow inoculation systems, a consolidated management practice that physically uncouples biological agents from toxic chemical seed treatments.

In the Brazilian politico-institutional scenario, the advancement of these biological matrices and circular bioeconomy systems is accompanied by recent regulatory frameworks, notably the enactment of Law No. 15.070/2024 and the establishment of Ordinance SDA/MAPA No. 1.270/2025. These instruments provide the necessary legal structuring and market security to the sector. However, the rapid expansion of on-farm production driven by this institutional environment raises technical alerts within the scientific community. Multiplication processes conducted in a rural area environment without rigorous control of asepsis and isolation present imminent risks of biological contamination and accidental dissemination of undesirable agents, highlighting the need for strict biosecurity parameters.

As future perspectives for the definitive consolidation of this biotechnological pathway, it is imperative that scientific research and the industrial sector direct efforts toward: (1) the selection and regionalization of autochthonous microorganisms adapted to local edaphoclimatic specificities; (2) the development of stable protective formulations, efficient carriers, and cellular encapsulation technologies; (3) the integration of microbiome-assisted plant breeding programs, focusing on the selection of soybean genotypes with high symbiotic affinity and optimized root exudation profiles. Recognizing that rhizosphere metabolites, particularly flavonoids, play a critical role in orchestrating the recruitment not only of rhizobia but also of AMF and a broader range of beneficial bacteria, future efforts must decipher these biochemical dialogues. Leveraging cutting-edge tools such as spatial transcriptomics and cell-type-specific CRISPR, alongside new insights into the Nodulation Signaling Pathway (NSP), will enable the targeted modulation of flavonoid metabolism. When these advanced genetic interventions are combined with the application of rationally designed Synthetic Communities (SynComs), it will be possible to fine-tune the stoichiometric C/N/P balance, fully optimizing multipartite interactions without imposing detrimental metabolic costs on the crop; (4) the establishment of structured technical frameworks that ensure the monitoring, laboratorization, and analytical standardization of rural biofactories.

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Abbreviations

The following abbreviations are used in this manuscript:

ABA	Abscisic Acid
ABC	ATP-Binding Cassette
ABC Plan	Plano Setorial para Adaptação à Mudança do Clima e Baixa Emissão de Carbono na Agropecuária
ABC+	Plano Setorial para Adaptação à Mudança do Clima e Baixa Emissão de Carbono na Agropecuária (2020–2030)
ACC	1-Aminocyclopropane-1-Carboxylate
ALMT	Aluminum-Activated Malate Transporter
AMF	Arbuscular Mycorrhizal Fungi
Aprosoja	Associação dos Produtores de Soja
APX	Ascorbate Peroxidase
ATP	Adenosine Triphosphate
BF	Biochar-based Structured Fertilizers
BNF	Biological Nitrogen Fixation
C	Carbon
CAT	Catalase
CBS	Circular Bioeconomy Systems
CEPs	C-terminally Encoded Peptides
CMN	Common Mycorrhizal Network
Co	Cobalt
CO_2	Carbon Dioxide
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
DHMC	4,4′-dihydroxy-2′-methoxychalcone
Embrapa	Empresa Brasileira de Pesquisa Agropecuária
EPS	Exopolysaccharides
Fe	Iron
GC-MS	Gas Chromatography–Mass Spectrometry
GDP	Gross Domestic Product
GHG	Greenhouse Gas
GPX	Glutathione Peroxidase
GR	Glutathione Reductase
GS	Glutamine Synthetase
HS	Humic Substances
IAA	Indole-3-Acetic Acid
IBA	Indole-3-Butyric Acid
IICA	Inter-American Institute for Cooperation on Agriculture
ISR	Induced Systemic Resistance
J2	Second-Stage Juveniles
K	Potassium
LPS	Lipopolysaccharides

M%	Mycorrhizal Colonization Intensity
MAPA	Ministério da Agricultura e Pecuária
MATE	Multidrug and Toxic Compound Extrusion
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate Reductase
Mn	Manganese
Mo	Molybdenum
N	Nitrogen
N_2	Atmospheric Nitrogen
N_2O	Nitrous Oxide
NADH-GOGAT	NADH-glutamate synthase
NH_3	Ammonia
NH_4^+	Ammonium
NO_3^-	Nitrate
NopP	Nodulation Outer Protein P
NSP	Nodulation Signaling Pathway
NTS	No-Tillage System
P	Phosphorus
Pb	Lead
PGPMs	Plant Growth-Promoting Microorganisms
PGPR	Plant Growth-Promoting Rhizobacteria
PHT1	Phosphate Transporter 1
Pi	Inorganic Orthophosphate
$PM_{2.5}$	Particulate Matter
PNB	Programa Nacional de Bioinsumos
PNPB	National Biodiesel Production and Use Program
POD	Peroxidase
PSB	Phosphate-Solubilizing Bacteria
SAR	Systemic Acquired Resistance
SDA	Secretaria de Defesa Agropecuária
SNPs	Single Nucleotide Polymorphisms
SOD	Superoxide Dismutase
SPAD	Soil–Plant Analysis Development
sRNAs	Small RNAs
SWEETs	Sugars Will Eventually be Exported Transporters
SynBio	Synthetic Biology
SynComs	Synthetic Communities
TBARS	Thiobarbituric Acid Reactive Substances
TOSS	Type Zero Secretion Systems
USA	United States of America
VOCs	Volatile Organic Compounds
Zn	Zinc

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