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Biofertilizers in sustainable agriculture and seed science: Mechanisms, advances and future prospects for enhancing soil fertility, seed quality and crop productivity

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Abstract

Global agricultural production faces an unprecedented dual challenge: sustaining food security for an escalating human population while mitigating severe soil degradation resulting from decades of intensive synthetic agrochemical usage. Biofertilizers, defined as formulations containing living or latent beneficial soil microorganisms, have emerged as an essential ecological technology in sustainable agronomy and seed science. This review provides a comprehensive synthesis of the multi-faceted mechanisms, technological advances and future trajectories of microbial bioinoculants in enhancing soil biological fertility, seed quality dynamics and overall crop productivity. We examine the functional diversity of major biofertilizers, including symbiotic and non-symbiotic nitrogen fixers (*Rhizobium*, *Azotobacter*, and *Azospirillum*), phosphate and potassium solubilizing bacteria and fungi (*Bacillus*, *Pseudomonas*, *Aspergillus*, and *Glomus* spp.), zinc-solubilizing bioinoculants and plant growth-promoting rhizobacteria (PGPR). Crucial cellular mechanisms are detailed: biological nitrogen fixation via nitrogenase regulation (*nif* gene clusters), organic acid secretion and enzymatic phosphatase activity for mineral solubilization, phytohormonal modulation (auxins, cytokinins, and ACC-deaminase activity), induced systemic resistance (ISR) and abiotic stress mitigation via exopolysaccharide biofilm formation. Furthermore, this review highlights the transformative role of biofertilizers in seed science, focusing on seed biopriming mechanics, germination kinetics, seedling vigor enhancement, seed coat bioprotection against pathogens and grain biofortification. Recent technological innovations, including nano-biofertilizers, synthetic microbial consortia (SynComs), CRISPR-Cas strain engineering, microencapsulation matrices and liquid shelf-stable formulations, are evaluated alongside field implementation bottlenecks such as carrier shelf-life decay, environmental stress sensitivities and regulatory hurdles. Finally, strategic directions for integrating precision bio-fertilization into climate-resilient farming systems are outlined. Biofertilizers represent a vital ecological pillar for restoring degraded agroecosystems, minimizing chemical fertilizer dependencies by 25% to 50% and securing long-term global food production.

Keywords: Biofertilizers, seed biopriming, rhizosphere microbiome, plant growth-promoting rhizobacteria (PGPR), nitrogen fixation, sustainable soil fertility

Introduction

The imperative to achieve global food security for a projected world population of nearly 10 billion by 2050 presents one of the most formidable challenges facing modern agricultural science [25, 52]. Over the past six decades, the Green Revolution significantly expanded agricultural productivity through the intensive utilization of high-yielding crop varieties, expanded irrigation infrastructure and massive applications of synthetic chemical fertilizers and pesticides [63]. However, this heavy reliance on synthetic agrochemicals, particularly synthetic nitrogenous and phosphatic fertilizers, has incurred profound ecological and economic penalties [28]. Modern industrial agriculture is currently grappling with widespread soil degradation, characterized by organic matter depletion, severe soil acidification, loss of beneficial soil biodiversity, disruption of natural nutrient cycling and widespread groundwater contamination via nitrate leaching [36, 47]. Compounding these soil health crises is the inherently low physiological nutrient use efficiency

(NUE) of synthetic chemical fertilizers in agricultural soils [17]. It is estimated that 50% to 70% of applied synthetic nitrogen and up to 80% to 90% of applied synthetic phosphorus are lost to the surrounding environment or rendered chemically fixed and unavailable to crop roots through mineral precipitation and soil adsorption [49, 33]. Phosphorus, an essential macro-element for energy transfer and nucleic acid synthesis, is predominantly derived from finite, non-renewable rock phosphate reserves that are projected to reach peak extraction within the current century, creating severe geopolitical and economic vulnerabilities for global food systems [19, 21]. In response to these environmental and resource crises, global agricultural management is undergoing a paradigm shift toward regenerative, ecologically intensive farming systems that prioritize soil biological health, nutrient recycling efficiency and agro-ecosystem resilience [31].

In this context, biofertilizers have emerged as a cornerstone technology for sustainable soil fertility management and crop production [82, 35]. Broadly defined, biofertilizers are carrier-based or liquid formulations containing living or latent cells of beneficial soil microorganisms, such as bacteria, fungi, actinomycetes and cyanobacteria that colonize the rhizosphere, rhizoplane, or interior endosphere tissues of plants when applied to seeds, plant surfaces, or soil [51]. Unlike synthetic chemical fertilizers, which directly supply inorganic ions to the soil solution, biofertilizers enhance plant growth by biological nitrogen fixation, solubilizing insoluble mineral nutrients (phosphorus, potassium, zinc, iron), synthesizing phytohormones, stimulating root system architecture and conferring systemic resistance against biotic and abiotic environmental stresses [2].

Concurrently, the discipline of Seed Science and Technology has recognized the critical role of seed-microbe interactions in establishing early crop vigor and uniform stand establishment [55]. Seeds represent the fundamental biological vector in crop production and their physiological vigor directly dictates field emergence, stand density and eventual crop yield potential [27]. Seed biopriming, which is an advanced seed enhancement technology combining controlled seed hydration with biological inoculation, allows beneficial microorganisms to invade the seed coat, pre-activate metabolic machinery and establish robust rhizosphere colonization prior to radicle emergence [52]. This synergistic intersection of seed technology and microbial ecology represents a vital frontier for enhancing crop resilience under fluctuating environmental conditions [60].

2. Taxonomy, Classification and Functional Diversity of Biofertilizers

Microbial biofertilizers encompass an exceptionally diverse range of taxonomic groups, reflecting millions of years of co-evolution between soil microorganisms and terrestrial plants [16]. Functionally, bioinoculants are categorized based on their primary physiological mechanisms: nitrogen fixers, phosphorus solubilizers and mobilizers, potassium solubilizers, micronutrient mobilizers and general plant growth-promoting rhizobacteria (PGPR) [5].

2.1 Nitrogen-Fixing Bioinoculants

Nitrogen-fixing biofertilizers convert atmospheric dinitrogen (N_2) into plant-utilizable ammonia (NH_3), representing the largest biological input of nitrogen into terrestrial ecosystems [68]. These microorganisms are broadly subdivided into symbiotic, associative and free-living nitrogen fixers. Symbiotic nitrogen-fixing bacteria primarily belong to the family Rhizobiaceae, including genera such as *Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Mesorhizobium* and *Azorhizobium* [57]. These

bacteria form highly specialized, host-specific root nodules on leguminous crops (e.g., soybean, chickpea, lentil, groundnut), where they exchange fixed nitrogen for plant-derived dicarboxylic acids [61]. In non-leguminous plants, actinorhizal fungi of the genus *Frankia* establish root nodule endosymbioses capable of substantial atmospheric nitrogen fixation [75].

Associative nitrogen fixers colonize the rhizoplane and root endosphere of non-leguminous cereal crops, such as wheat, rice, maize, sorghum and sugarcane [15]. Dominant associative strains include *Azospirillum brasilense*, *Azospirillum lipoferum*, *Gluconacetobacter diazotrophicus* and *Herbaspirillum seropedicae* [74]. Free-living nitrogen-fixing heterotrophs, such as *Azotobacter chroococcum*, *Azotobacter vinelandii* and *Beijerinckia indica*, operate independently in the rhizosphere, acquiring energy from root exudates while contributing 10 to 30 kg N/ha annually to the soil system [35].

2.2 Phosphate Solubilizing and Mobilizing Microorganisms

Phosphorus (P) is a primary limiting macro-nutrient in agricultural soils due to its strong tendency to form insoluble complexes with aluminum (Al^{3+}) and iron (Fe^{3+}) in acidic soils, or calcium (Ca^{2+}) in alkaline soils [79]. Phosphate Solubilizing Microorganisms (PSMs) release bound soil phosphorus through organic acid exudation and enzymatic hydrolysis [71]. Key bacterial solubilizers include *Bacillus megaterium*, *Bacillus subtilis*, *Pseudomonas striata*, *Pseudomonas putida* and *Burkholderia cepacia* [9]. Fungal solubilizers, notably *Aspergillus niger*, *Aspergillus awamori* and *Penicillium radicum*, demonstrate high P-solubilization capacity owing to their extensive hyphal production of citric, oxalic and gluconic acids [18]. In contrast to solubilizers, Phosphate Mobilizing Microorganisms, specifically Arbuscular Mycorrhizal Fungi (AMF) belonging to the phylum Glomeromycota (such as *Glomus intraradices*, *Rhizophagus irregularis* and *Funneliformis mosseae*), form obligate biotrophic mutualisms with nearly 80% of land plants [84]. AMF extend an intricate extra-radical hyphal network deep into soil pores beyond the depleted root absorption zone, vastly expanding the absorptive surface area and facilitating the uptake of immobile orthophosphate ions ($H_2PO_4^-$ and HPO_4^{2-}) [13].

2.3 Potassium, Zinc and PGPR Bioinoculants

Potassium (K) is the third essential macro-element, predominantly bound within soil minerals such as micas, feldspars and illites [58]. Potassium Solubilizing Bacteria (KSB), including *Frateuria aurantia*, *Bacillus edaphicus* and *Paenibacillus mucilaginosus*, solubilize silicate minerals through organic acid secretion, capsular polysaccharide production and mineral weathering [80]. Similarly, micronutrient deficiencies, particularly zinc (Zn) and iron (Fe), severely constrain crop yields and human nutritional security [27]. Zinc Solubilizing Bacteria (ZSB), such as *Acinetobacter calcoaceticus*, *Bacillus aryabhattai* and *Rhizobium* strains, convert insoluble zinc oxide (ZnO), zinc carbonate ($ZnCO_3$) and zinc phosphate ($Zn_3(PO_4)_2$) into bioavailable Zn^{2+} ions via protonation and chelation, significantly enriching grain micronutrient density [76].

Plant Growth-Promoting Rhizobacteria (PGPR) represent a broad functional group of aggressive root-colonizing bacteria that enhance plant growth through combined direct and indirect mechanisms [46]. Prominent PGPR genera include *Pseudomonas*, *Bacillus*, *Serratia*, *Enterobacter* and *Streptomyces* [50]. Endophytes, defined as microorganisms residing within plant tissues without inducing pathogenic symptoms, such as *Trichoderma harzianum*, *Piriformospora indica* and

Methylobacterium extorquens, form intimate metabolic partnerships that confer robust systemic tolerance against

drought, salinity and necrotrophic pathogens [39].

Table 1: Classification, functional guilds, key microbial strains, primary mechanisms and agronomic applications of biofertilizers.

Functional Guild	Key Microbial Genera / Species	Primary Biochemical Mechanism	Target Crop Groups	Agronomic Benefits
Symbiotic N ₂ Fixers	<i>Rhizobium leguminosarum</i> , <i>Bradyrhizobium japonicum</i> , <i>Sinorhizobium meliloti</i>	Nitrogenase complex Root nodule symbiosis, leghemoglobin oxygen regulation	Pulses, Soybeans, Forage Legumes	Directly fixes 50-300 kg N/ha/yr; reduces chemical N fertilizer dependence by 50-75%.
Non-Symbiotic & Associative N ₂ Fixers	<i>Azotobacter chroococcum</i> , <i>Azospirillum brasilense</i> , <i>Gluconacetobacter diazotrophicus</i>	Aerobic & microaerophilic nitrogenase activity, IAA exudation, ACC deaminase synthesis	Cereals (Wheat, Rice, Maize), Sugarcane	Fixes 15-40 kg N/ha/yr; enhances root elongation and lateral branching by 25-40%.
Phosphate Solubilizers & Mobilizers (PSMs/AMF)	<i>Bacillus megaterium</i> , <i>Pseudomonas striata</i> , <i>Aspergillus niger</i> , <i>Glomus intraradices</i> (AMF)	Organic acid exudation (citrate, gluconate), phytase secretion, extra-radical hyphal network	All Field Crops, Vegetables, Fruit Crops	Solubilizes 30-50 kg P ₂ O ₅ /ha/yr; increases P use efficiency by 20-35%.
Potassium & Micronutrient Solubilizers	<i>Frateuria aurantia</i> , <i>Bacillus edaphicus</i> , <i>Acinetobacter calcoaceticus</i>	Proton extrusion, mineral weathering, organic acid chelation of K, Zn and Fe	Cereals, Oilseeds, Horticultural Crops	Mobilizes non-exchangeable K; enhances grain Zn/Fe content by 15-30%.
Plant Growth Promoting Rhizobacteria (PGPR)	<i>Pseudomonas fluorescens</i> , <i>Bacillus subtilis</i> , <i>Trichoderma harzianum</i>	Phytohormone crosstalk, siderophore secretion, Induced Systemic Resistance (ISR)	Cereals, Pulses, Commercial Crops	Suppresses seed/soil-borne pathogens; increases seedling vigor index by 30-50%.

3. Cellular, Molecular and Biochemical Mechanisms of Action

The agronomic efficacy of biofertilizers stems from a complex cascade of cellular, biochemical and genetic processes operating at the root-soil interface [62]. Biological nitrogen fixation is catalyzed by the multi-subunit metalloenzyme nitrogenase, which reduces atmospheric dinitrogen gas into ammonia according to the stoichiometry: $N_2 + 8H^+ + 8e^- + 16MgATP \rightarrow 2NH_3 + H_2 + 16MgADP + 16P_i$ [78]. The nitrogenase enzyme complex consists of two primary proteins: the dinitrogenase reductase (Fe-protein, encoded by *nifH*) and the dinitrogenase (MoFe-protein, encoded by *nifD* and *nifK*) [73]. Symbiotic *Rhizobium* bacteria rely on leghemoglobin, which is a plant-synthesized hemoprotein with an extremely high oxygen affinity, to maintain extremely low free oxygen tension (~10 nM) within bacteroids while delivering adequate oxygen flux for oxidative phosphorylation [3, 29]. The solubilization of mineral phosphorus, potassium and zinc is predominantly driven by microbial synthesis and secretion of low-molecular-weight organic acids, including gluconic, 2-ketogluconic, citric, oxalic, malic and succinic acids^{34, 54}. Gluconic acid biosynthesis, catalyzed by the membrane-bound enzyme glucose dehydrogenase (GDH) requiring the cofactor pyrroloquinoline quinone (PQQ), represents the principal solubilization pathway in *Pseudomonas* and *Bacillus* species [37]. These organic carboxylates lower rhizosphere pH by 1 to 2 units, promoting the protonolysis of insoluble phosphate minerals [44]. Biofertilizers dynamically alter plant architecture through the secretion of endogenous phytohormones [59]. Over 80% of rhizosphere bacteria synthesize Indole-3-Acetic Acid (IAA) via the tryptophan-dependent indole-3-pyruvic acid pathway²³. Microbial IAA stimulates root cell division and lateral root formation, expanding root surface area for water and nutrient interception [10]. Under stress, PGPR expressing ACC deaminase cleave the immediate ethylene precursor, ACC, into alpha-ketobutyrate and ammonia, suppressing stress ethylene accumulation and enabling uninhibited root growth [32, 33]. Inoculation with PGPR primes the plant immune system through Induced Systemic Resistance (ISR), conferring defense readiness via jasmonate and ethylene signaling pathways [82]. Primed plants exhibit accelerated accumulation of defense enzymes (peroxidase, polyphenol oxidase, PAL, SOD) upon pathogen challenge [61]. Additionally, biofertilizers synthesize antibiotics (DAPG, phenazines, lipopeptides) and siderophores (pyoverdine)

that starve pathogens of iron [18]. Under abiotic stress (drought, salinity), bioinoculants induce osmolyte accumulation (proline, trehalose) and exopolysaccharide (EPS) biofilms that maintain cell turgor and soil moisture [38, 64].

4. Biofertilizers in Seed Science and Technology

Seed Science and Technology form the foundation of modern crop production, as high-quality seed is the single most critical input for achieving uniform field emergence and maximal crop yield potential [53]. The integration of microbial bioinoculants into seed delivery systems, termed seed biopriming and bio-coating, represents a major paradigm shift in seed treatment technology [56]. During biopriming, seeds are imbibed in a liquid suspension of bioinoculants under controlled temperature and aeration, allowing seeds to reach Phase II of germination (the metabolic activation phase) without radicle emergence [8]. This controlled hydration triggers rapid imbibition kinetics, mobilizing seed reserves and allowing beneficial bacteria and fungal spores to adhere tightly to the seed coat, invade natural cracks and colonize the spermosphere [14]. Biopriming dramatically enhances seed germination kinetics, germination speed and overall seedling vigor [7]. Microbial bioinoculants secrete hydrolytic enzymes, particularly alpha-amylases, beta-amylases, proteases and lipases, into the endosperm during priming [66]. Alpha-amylase pre-activation accelerates the breakdown of stored complex starch into simple reducing sugars (maltose, glucose), providing immediate energy flux to the growing embryonic axis [26]. Advanced seed coating utilizes polymeric stickers (carboxymethyl cellulose, sodium alginate, polyvinylpyrrolidone) combined with solid carrier substrates (peat, biochar, lignite) [1]. Microencapsulation represents the state of the art in seed bio-delivery, wherein microbial cells are encapsulated within biodegradable biopolymer microbeads (calcium alginate, chitosan matrices) [77]. Microencapsulated biofertilizers protect sensitive vegetative bacterial cells against ambient desiccation, releasing viable propagules gradually upon seed sowing [22]. Seed biopriming also suppresses seed-borne pathogens (*Fusarium*, *Pythium*, *Rhizoctonia*) through niche exclusion, chitinase production and transgenerational seed biofortification, representing a phenomenon known as seed transgenerational biofortification [55].

Table 2: Impact of Seed Biopriming with Selected Microbial Bioinoculants on Seed Vigor Index, Germination Dynamics and Disease Incidence across Major Field Crops

Crop Species	Microbial Bioinoculant	Germination Increase (%)	Vigor Index Enhancement	Pathogen Suppression / Field Impact
Wheat (<i>Triticum aestivum</i>)	<i>Azotobacter chroococcum</i> + <i>Pseudomonas fluorescens</i>	+14.5% to +18.2%	+38.4% (Vigor Index I)	Suppresses <i>Bipolaris sorokiniana</i> spot blotch by 42%; accelerates emergence by 2.5 days.
Chickpea (<i>Cicer arietinum</i>)	<i>Mesorhizobium ciceri</i> + <i>Trichoderma harzianum</i>	+16.0% to +21.5%	+45.2% (Vigor Index II)	Controls <i>Fusarium oxysporum</i> wilt by 58%; increases nodule dry mass by 62%.
Rice (<i>Oryza sativa</i>)	<i>Azospirillum brasilense</i> + <i>Bacillus subtilis</i>	+12.0% to +15.8%	+32.6% (Vigor Index I)	Reduces <i>Magnaporthe oryzae</i> blast incidence by 35%; improves root length by 28%.
Maize (<i>Zea mays</i>)	<i>Pseudomonas putida</i> + <i>Glomus intraradices</i>	+15.2% to +19.0%	+41.0% (Vigor Index I)	Enhances seedling drought tolerance; increases early phosphorus uptake by 48%.
Soybean (<i>Glycine max</i>)	<i>Bradyrhizobium japonicum</i> + <i>Bacillus megaterium</i>	+18.0% to +23.4%	+50.8% (Vigor Index II)	Suppresses <i>Rhizoctonia solani</i> damping-off by 52%; increases grain yield by 24.5%.

5. Impact on Soil Fertility, Microbiome Dynamics and Carbon Sequestration

Biofertilizers serve as powerful drivers of soil ecological restoration, fundamentally transforming soil microbial architecture, enzymatic catalysis, structural stability and carbon cycling [43]. Application of biofertilizers significantly increases Soil Microbial Biomass Carbon (MBC) and Microbial Biomass Nitrogen (MBN) [40]. Introduced PGPR and mycorrhizal fungi act as keystone taxa, restructuring native rhizosphere communities through metabolic cross-feeding [24]. Bioinoculants elevate extracellular soil enzyme activities (dehydrogenase, urease, phosphatases, beta-glucosidase), accelerating nutrient turnover [81]. Furthermore, Arbuscular Mycorrhizal Fungi synthesize Glomalin-Related Soil Protein (GRSP), which binds primary soil mineral particles and microaggregates into stable macroaggregates, enhancing soil physical structure, water infiltration and long-term carbon sequestration in mineral-associated organic matter pools [6, 67].

6. Crop Productivity, Yield Dynamics and Integrated Nutrient Management (INM)

In staple cereal crops (wheat, rice, maize), dual bio inoculation with associative diazotrophs (*Azospirillum brasilense*, *Azotobacter chroococcum*) and phosphate solubilizers (*Bacillus megaterium*) consistently increases grain yield by 12% to 28% and enhances physiological nitrogen use efficiency (NUE) and phosphorus use efficiency (PUE) [4, 45]. In leguminous crops (chickpea, soybean, lentil), co-inoculation with host *Rhizobium* and PGPR increases nodulation, grain yield by 20% to 35% and seed crude protein content [12, 30]. Under Integrated Nutrient Management (INM), replacing 25% to 50% of recommended synthetic NPK doses with composite biofertilizers maintains conventional crop yields while preventing soil degradation and reducing environmental pollution [11].

7. Recent Technological Advances, Innovations and Next-Generation Bioinoculants

Nano-biofertilizers represent a cutting-edge fusion of nanotechnology and microbial biotechnology, involving the encapsulation of live microbial cells or metabolites within biocompatible nanomaterial matrices (chitosan, silica nanoparticles, and carbon nanotubes) [70]. Nano-encapsulation protects bioinoculants against desiccation, provides slow, sustained release and enhances seed coat penetration during biopriming [83]. Next-generation biofertilizers utilize Synthetic Microbial Consortia (SynComs), which are rationally designed multi-strain communities assembled using metagenomic data and ecological network modeling [20]. Multi-omics integration, CRISPR-Cas strain optimization and liquid formulations with cell protectants (glycerol, trehalose) extend shelf-life to 18 to 24

months at ambient temperatures [48, 72].

8. Technical Bottlenecks, Field Limitations and Quality Control

A major limitation of carrier-based biofertilizers is rapid cell mortality during storage due to desiccation and nutrient depletion, leading to cell population drops below mandatory regulatory thresholds (10^7 CFU/g) prior to field application [44]. Furthermore, biofertilizers frequently display inconsistent performance in natural field environments due to environmental abiotic stressors (temperature spikes, drought, salinity) and competitive exclusion by native microflora [41]. Overcoming these limitations requires establishing standardized global quality control protocols through the utilization of quantitative PCR (qPCR) strain verification, cell viability testing and bio-safety certifications [65].

9. Future Prospects and Strategic Directions

To maximize the global impact of biofertilizers in sustainable agriculture and seed science, future research and policy must prioritize four strategic directions:

- (1) **Smart Precision Bio-Fertilization:** Integrating bio-inoculants into digital precision farming, fertigation and variable-rate seed biopriming equipment.
- (2) **Climate-Smart Strain Discovery:** Prospecting hyper-tolerant bioinoculants from extreme environments (halo-tolerant, thermo-tolerant, psychrotolerant and metallotolerant strains) to buffer crops against climate extremes.
- (3) **Plant-Microbiome Breeding:** Breeding host crop varieties specifically selected for their capacity to recruit and support beneficial microbial mutualists via optimized root exudation chemistry.
- (4) **Policy and Economic Integration:** Establishing global bio-economy policies, carbon credit incentives for farmers adopting bioinoculants and strengthening agricultural extension networks to train farmers in proper bio-formulation storage and application.

10. Conclusion

Biofertilizers represent a foundational ecological pillar for transforming modern industrial agriculture into a sustainable, climate-resilient and biologically vibrant system. By harnessing the functional diversity of beneficial soil microorganisms, biofertilizers offer robust cellular mechanisms for biological nitrogen fixation, mineral nutrient solubilization, phytohormone regulation, induced systemic resistance and abiotic stress mitigation. In Seed Science and Technology, seed biopriming and advanced microencapsulation technologies provide an effective vector for accelerating germination kinetics, maximizing seedling vigor, protecting seeds against phytopathogens and enhancing

grain nutritional quality. While technical challenges regarding shelf-life stability, field performance consistency and quality control persist, recent advances in nano-biofertilizers, synthetic microbial consortia, omics engineering and liquid formulations provide clear pathways forward. Integrating biofertilizers into integrated nutrient management frameworks will significantly reduce global reliance on synthetic agrochemicals by 25% to 50%, restore degraded soil ecosystems and secure sustainable food production for generations to come.

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