

Microbial inoculants – fostering sustainability in groundnut production

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Kaviya Sree Krishnan^{1,*} , Anandham Rangasamy^{1,*} ,
Yuvasri Errakutty Arunan^{1,*} , Balachandar Dananjeyan¹,
Thiyageshwari Subramaniam² and Vincent Saminathan³

Abstract

Groundnut (*Arachis hypogaea* L.) is a vital leguminous oilseed crop, widely cultivated in tropical and subtropical regions due to its high nutritional and economic significance in food, feed, and oil purposes. It is a rich source of protein, oil, vitamins, minerals, and bioactive compounds with anti-inflammatory, anticancer, and anti-aging properties. Globally, groundnut production is approximately 54.2 million tonnes, with India contributing 10.1 million tonnes through rainfed cultivation. However, its productivity is constrained by drought, salinity, soil nutrient deficits, and disease infestations. Conventional farming depends on chemical inputs to enhance yield and productivity but negatively impacts soil health and fertility, reduces microbial diversity, and pollutes agroecosystems, creating an urgent need for sustainable alternatives. Microbe-based bioinoculants comprising nitrogen-fixers, phosphorus solubilizers, potassium solubilizers, sulphur oxidizers, other plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and cyanobacteria offer an alternative approach to enhance the growth and yield of groundnut through various direct and indirect mechanisms, including augmenting nutrient absorption, improving quality parameters, suppressing plant pathogens, stimulating plant defence, and increasing resilience to abiotic stresses. This narrative review examines the

¹Department of Agricultural Microbiology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

²Department of Soil Science and Agricultural Chemistry, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

³Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India

*These authors contributed equally to this work.

Corresponding author:

Rangasamy Anandham, Department of Agricultural Microbiology, Tamil Nadu Agricultural University, Coimbatore 641003, Tamil Nadu, India.

Email: anandhamranga@gmail.com



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diversity, benefits, and growth-promoting mechanisms of rhizospheric, phyllospheric, and endophytic microorganisms associated with groundnut. Additionally, molecular docking of groundnut root exudate metabolites, produced upon microbial inoculation, with stress-responsive proteins highlights the significance of microbial inoculants in mitigating drought and salinity stresses. This review synthesizes recent advances in microbial inoculant applications, highlighting their potential to revolutionize sustainable groundnut cultivation. Therefore, microbial inoculants provide a promising solution ensuring sustainability and assurance of food security amid global difficulties.

Keywords

Groundnut, bioinoculant, rhizosphere, endophytes, phyllosphere, root exudates, abiotic stress

Introduction

Groundnut (*Arachis hypogaea* L.), or peanut, is a vital leguminous and oilseed crop of the *Fabaceae* family, widely grown in tropical and subtropical regions for its nutritional and economic significance. It is rich in protein (25 g), oil (47–53%), and vitamins such as B1 (0.64 mg), B3 (12 mg), B5 (1.76 mg), B6 (0.34 mg), B9 (240 µg), E (8.33 mg) and minerals such as magnesium (168 mg), calcium (92 mg), phosphorus (76 mg), iron (4.58 mg) and zinc (3.27 mg) approximately per 100 g of seed. It also contains bioactive compounds including flavonoids, resveratrol, and phytosterols possessing antioxidant, anti-inflammatory, anticancer, and anti-aging properties.^{1,2} Beyond human consumption, it serves as a key source of edible oil, the food industry (peanut butter, confectionery, snacks, protein supplements), livestock fodder, and soil fertility enhancement through nitrogen fixation, reducing dependence on synthetic fertilizers.³

Global groundnut production reached approximately 54.2 million tonnes across 30.5 million hectares, with China leading at 18.3 million tonnes, followed by India at 10.1 million tonnes exporting 680.70 thousand metric tonnes in 2023–2024 (860.68 million USD).^{4,5} In India, groundnut cultivation is predominantly rainfed, with the *Kharif* season (June to October) accounting for the largest cultivated area (about 4000 hectares) and the highest production (around 8000 tonnes), compared to the *Rabi* and summer seasons. Figure 1 illustrates the recent trends in groundnut cultivation, production, and derived products from global and Indian perspectives. Since *Kharif* cultivation relies heavily on monsoon rainfall, any variation in precipitation patterns can lead to drought, adversely impacting germination, biomass accumulation, and pod development subjecting to 85% yield loss in groundnut estimated at 50 million United States Dollars (USD) annually, particularly in arid and semi-arid regions.⁶ Soil salinity and nutrient deficiency further exacerbate these issues by causing osmotic stress, nutrient imbalances, and ion toxicity, ultimately leading to poor plant growth and yield losses of 53.6% and 40%, respectively.^{7,8} Moreover, inadequate soil fertility, recurrent pest occurrences, and opportunistic pathogen breakouts could profoundly affect the crucial growth stages of groundnut, such

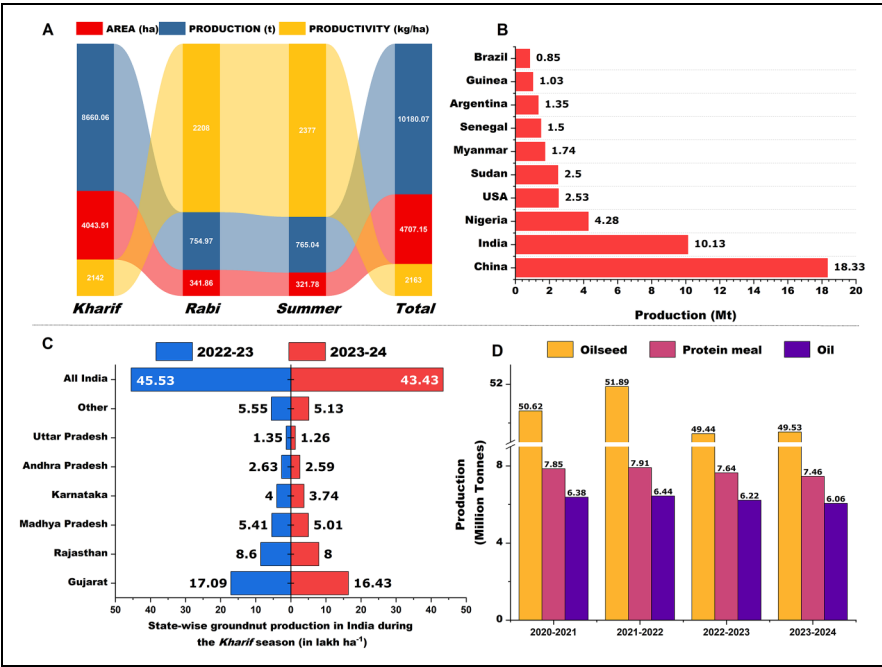


Figure I. Trends in groundnut cultivation, production, and derived products: global and Indian perspectives. Panel (A) illustrates the seasonal distribution of groundnut cultivation in India, showcasing variations in area, production, and productivity across the Kharif, Rabi, and summer seasons. Panel (B) presents a global comparison of groundnut production, highlighting China and India as the leading producers. Data for both panels were obtained from FAOSTAT, 2024 (<https://www.fao.org/faostat/en/#data/QCL>). Panel (C) provides a state-wise analysis of groundnut production in India during the Kharif season over two consecutive years (source: Angrau groundnut outlook report – June to May 2023-24 – search). Panel (D) depicts trends in groundnut-derived products, including oilseed, protein meal, and oil, indicating fluctuations in production over recent years (source: <https://www.fas.usda.gov/data/oilseeds-world-markets-and-trade-02112025>).

as flowering, peg formation, and pod development, impeding nutrient absorption and diminishing overall output.⁹ Hence, there is an urgent need to develop an alternative sustainable approach to strengthen soil health and overall groundnut productivity.

In response to increasing food demand, modern agriculture has relied heavily on chemical fertilizers to enhance crop yields. Chemical inputs dominate because of their cost, widespread accessibility, and immediate effect in supporting crop productivity. For groundnut, the recommended NPK fertilizer application is 25:75:25 kg/ha, which yields an oil yield of 49.94% and a dry pod yield of about 2605.78 kg/ha.¹⁰ However, excessive use of chemical fertilizers has led to environmental degradation, including soil nutrient depletion, contamination of soil and water resources, and loss of soil microbial diversity.¹¹ Continuous fertilization alters soil pH, disrupts microbial communities,

and reduces the bioavailability of essential nutrients, ultimately decreasing crop productivity.¹² Moreover, unsustainable land use practices contribute to land degradation, climate change, and global warming, adversely affecting crop growth, yield, and overall agricultural sustainability.¹³

To mitigate these issues, sustainable agricultural practices incorporating organic amendments and microbial-based bio-inoculants have emerged as viable alternatives. These microbial inoculants enhance soil health, improve nutrient mobilization and solubilization, and promote plant growth while reducing reliance on chemical inputs.^{14,15} Compared to chemical fertilizers, microbial inoculants nurture soil health by improving its structure and aggregation, nutrient cycling regulating pH, supporting soil microbial communities, enriching fertility by organic matter decomposition, and aiding in heavy metal degradation.^{16,17} The use of microbial inoculants in agriculture began during the 19th and 20th centuries with the discovery of *Rhizobium* in leguminous crops which was later purified and patented first by Nobbe and Hiltner in 1896 which laid the foundation for the commercialisation of microbial inoculants and their application in crop cultivation.¹⁸ Nitrogen fixers, phosphorus solubilizers, potassium mobilizers, and plant growth enhancers such as plant growth-promoting rhizobacteria (PGPR), mycorrhizal fungi, and cyanobacteria improve groundnut productivity. Beneficial strains of microorganisms such as *Rhizobium phaseoli* S18, *Rhizobium pusense* S6R2, *Pantoea dispersa* YBB19B, *Enterobacter cloacae* S23, and *Bacillus tequilensis* NBB13 enhance nutrient acquisition, stimulate phytohormone synthesis, improve stress tolerance, and act as bio-control agents against pathogens by producing antibiotics, lytic enzymes, hydrogen cyanide (HCN), bacteriocins, ACC (1-aminocyclopropane-1-carboxylate) deaminase, and siderophores.^{19–21} They also compete with pathogens for resources and induce systemic resistance in plants, thereby mitigating infections and promoting overall plant health.²² Microbial inoculants are applied through seed treatment, seedling root immersion, soil application, or foliar spray to ensure efficient colonization and optimal plant growth. These methods enhance nutrient uptake, improve soil fertility, and contribute to long-term agricultural sustainability.²³

Despite extensive research on microbial inoculants in agriculture, there is still a lack of comprehensive reviews detailing their effectiveness in groundnut cultivation. This review explores the microbial diversity, benefits, and mechanisms by which functional microbial groups such as rhizosphere bacteria, phyllosphere bacteria, endophytic bacteria, mycorrhizal fungi, and cyanobacteria contribute to groundnut productivity. Furthermore, it investigates how microbial inoculants influence root exudate metabolites, which interact with stress-responsive proteins under saline and drought conditions. Understanding these microbe-plant interactions through molecular docking and functional analysis provides insights into improving groundnut production under challenging agro-climatic conditions. This narrative review offers a holistic perspective on the potential of microbial inoculants in addressing key challenges in groundnut cultivation, reinforcing their role in enhancing plant growth, resilience, and overall agricultural sustainability.

This review is based on an extensive literature search (2000–2024) across databases including Google Scholar, PubMed, ScienceDirect, SpringerLink, and CAB Abstracts, following the SANRA guidelines for narrative reviews.²⁴ Key search terms such as

‘microbial inoculants’, ‘groundnut-associated microorganisms’, ‘plant growth promotion’, ‘soil health improvement’, and ‘stress alleviation’ were utilized. Nearly 50 peer-reviewed articles, book chapters, and conference materials were analysed to examine the role of beneficial microbes in sustainable groundnut production.

Microorganisms associated with groundnut

The microbial diversity of groundnuts is crucial as it enhances their growth and development under diverse stress circumstances and increases soil quality.²⁵ These encompass multiple bacterial and fungal taxa recognized for their roles in nitrogen fixation, phosphate solubilization, disease suppression, and growth enhancement.^{19,26} This diversity includes both culturable and unculturable bacteria that exert different influences on groundnut development. Understanding groundnut-associated microbial diversity is essential for identifying nitrogen fixers, phosphate solubilizers, plant growth-promoting endophytes, rhizobacteria, and stress-resilient microbes. These microbes enhance soil health, induce systemic resistance, and reduce reliance on synthetic fertilizers, promoting sustainable agriculture.^{27,28} Figure 2 represents the role of beneficial microorganisms in promoting groundnut growth and sustainability.

Plants interact with diverse microbial communities that inhabit different ecological niches, including the rhizosphere (root-associated microbes), phyllosphere (leaf-associated microbes), and endophytes (microbes residing within plant tissues). Among these, culturable microorganisms that can be isolated and developed using specific media constitute a

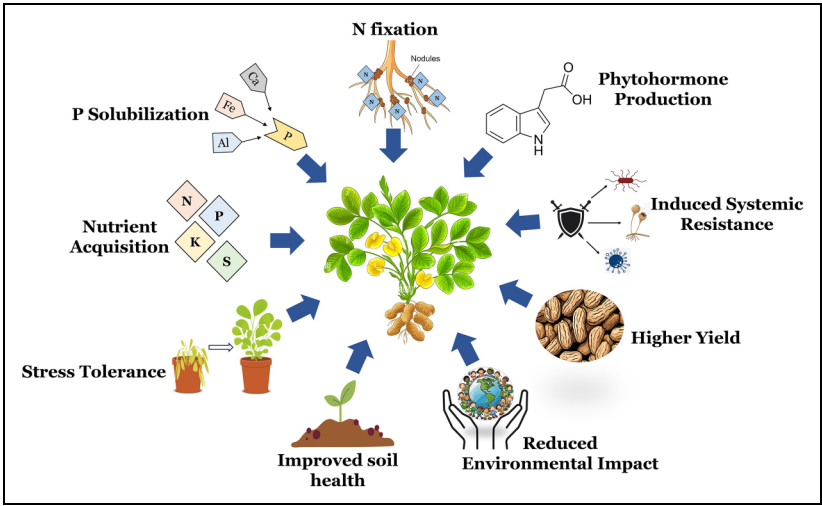


Figure 2. Role of beneficial microorganisms in groundnut growth and sustainability microbial inoculants promote groundnut growth and sustainability through nitrogen fixation, phosphorus solubilization, nutrient acquisition, phytohormone production, induced systemic resistance, stress tolerance, improved soil health, higher yield, and reduced environmental impact.

minor yet significant fraction of microbial diversity.²⁹ Despite their limited representation, they play a crucial role in elucidating direct plant-microbe interactions. Several nitrogen-fixing bacteria, such as *Rhizobium* and *Bradyrhizobium*, have been isolated from root nodules (Table 1). Similarly, methylophilic bacteria, including *Pseudomonas* and *Bacillus*, have been identified in the phyllosphere, stems, and root zones, exhibiting plant growth-promoting attributes that enhance groundnut growth under field conditions.^{29,30}

Microbial diversity includes a vast array of uncultivable microorganisms, such as bacteria, archaea, and fungi, that cannot be cultured under laboratory conditions.³¹ Consequently, various methodologies such as metagenomics, next-generation sequencing (NGS) (including Illumina and PacBio), 16S rRNA and ITS sequencing, shotgun metagenomics, metatranscriptomics, and metaproteomics were employed to elucidate the presence of both culturable and unculturable microorganisms associated with groundnut rhizosphere soil, as well as to identify the functional genes within the microbial communities and their roles in nutrient cycling, stress resistance, and disease suppression.^{32,33}

Rhizospheric bacteria

The rhizosphere is the area surrounding plant roots where exudates are released by the plants, affecting microorganism interactions and enhancing plant development and yield. Rhizosphere bacteria promote plant growth in many ways, hence diminishing the need for chemical fertilizers.⁴² The rhizosphere of groundnut contains a diverse array of microbes, including bacteria, fungi, actinobacteria, and other microbial entities. The structure and behaviour of microbial communities in the groundnut rhizosphere, together with their beneficial features, must be confirmed by pot cultures and field trials

Table 1. List of rhizobia nodulating groundnut.

Nodulating microorganisms	Geographic origin	References
<i>Rhizobium giardinii</i>	Argentina	34
<i>Rhizobium leguminosarum</i>	Egypt	25
<i>Rhizobium tropici</i>	Argentina	34
<i>Rhizobium phaseoli</i>	India	19
<i>Rhizobium mayense</i>	India	19
<i>Rhizobium pakistanensis</i>	Pakistan	35
<i>Bradyrhizobium lablabi</i>	China	36
<i>Bradyrhizobium arachidis</i>	China	37
<i>Bradyrhizobium subterraneum</i>	Namibia	38
<i>Bradyrhizobium vignae</i>	Namibia	39
<i>Bradyrhizobium nanningense</i>	China	40
<i>Bradyrhizobium guangzhouense</i>	China	40
<i>Bradyrhizobium zhanjiangense</i>	China	40
<i>Bradyrhizobium guangdongense</i>	China	41
<i>Bradyrhizobium guangxiense</i>	China	41

to create prospective bioinoculants. The rhizosphere of groundnut was predominantly composed of the phyla *Actinomycetota* (formerly *Actinobacteria*), *Pseudomonadota* (formerly *Proteobacteria*), *Saccharibacteria*, *Chloroflexota* (formerly *Chloroflexi*), *Acidobacteriota* (formerly *Acidobacteria*), and *Cyanobacteriota* (formerly *Cyanobacteria*). In drought-impacted soils, the populations of *Actinomycetota* and *Acidobacteriota* increased throughout the seedling and pod development phases, whereas *Cyanobacteriota* and *Gemmatimonadota* (formerly *Gemmatimonadetes*) proliferated during the flowering phase.⁴³ The mature groundnut rhizosphere displayed an increased abundance of *Gammaproteobacterota*, *Bacillota*, and the *Bacteroidota* (formerly *Cytophaga-Flavobacteria-Bacterioides*) group, but the *Rhizobiaceae* family of *Pseudomonadota* was absent.⁴⁴ The research assessed the microbial community of the groundnut rhizosphere and geocarposphere (soil region surrounding developing pod) by 16S rRNA amplicon sequencing, revealing a higher abundance of *Acidobacteriota* that facilitated seed germination. In contrast, *Pseudomonadota*, *Actinomycetota*, and the species of *Dyella* and *Burkholderia* exhibited greater abundance in the rhizosphere.⁴⁵ In the seed germination phase, *Pseudomonas indica* predominated, but *Bacillus* was more prevalent during the vegetative stage in the groundnut rhizosphere.³¹ *Rhizobium giardinii* NET30 and *Rhizobium tropici* NCHA22 were identified as fast proliferators of rhizobia.³⁴ *Enterobacter arachidis* Ah-143 isolated from the groundnut rhizosphere, contains the *nifH* gene that facilitates atmospheric nitrogen fixation.⁴⁶ Co-inoculation of rhizosphere isolates *Serratia marcescens* EG 10 and *Trichoderma harzianum* with *Bradyrhizobium* sp. USDA 3456, led to enhanced vegetative growth, nodule numbers, and pod yield through plant growth-promoting activities such as indole acetic acid production, siderophore synthesis, and phosphorus solubilization.⁴⁷

Endophytic bacteria

Endophytes are microorganisms that live either inside the plant tissues either intercellularly or extracellularly, without harming the host plants.⁴⁸ The bacteria linked to groundnut found in root nodules are essential for plant growth, nutrient uptake, stress mitigation, and disease suppression. These microorganisms are specialized for particular plant tissues, forming mutualistic partnerships that confer essential advantages to the host plant, which are vital for sustainable agricultural methods.⁴⁹ Groundnut root nodules contain a diverse array of endophytic microorganisms, including rhizobial endophytic (RE) bacteria and non-rhizobial endophytic (NRE) bacteria, also known as passenger endophytes (PE), which inadvertently enter the nodule and are regarded as potential biofertilizers and biocontrol agents. Root nodules are specialized structures resulting from the symbiotic relationship between bacteria and the host plant, mostly housing nitrogen-fixing bacteria, particularly *Rhizobium* and *Bradyrhizobium*.²⁵ They transform atmospheric nitrogen (N_2) into ammonia (NH_3), which is accessible for plant absorption to produce amino acids and proteins.

Research on groundnut nodule endophytes indicated that these microorganisms were classified into the phyla *Alphaproteobacterota*, *Betaproteobacterota*, *Gammaproteobacterota*, and *Bacillota*. The groundnut encompasses various non-rhizobial endophytic genera,

including *Agrobacterium*, *Pantoea*, *Bacillus*, *Herbaspirillum*, *Burkholderia*, *Mitsuraria*, *Methylobacterium*, *Pseudomonas*, *Enterobacter*, and *Klebsiella*. These endophytes exhibit plant growth-promoting characteristics that augment crop development and represent potential bioinoculants for sustainable groundnut agriculture.^{19,30} Among the 98 bacterial isolates, the majority belongs to the phyla *Pseudomonadota* comprising *Alphaproteobacterota* (3), *Betaproteobacterota* (3), and *Gammaproteobacterota* (45) as well as *Bacillota* (44) and *Bacteroidota* (3). Among these, 58 endophytic bacteria were associated with the bunching type of groundnut (VRI 2), while 40 were linked to the semi-spreading phenotype (VRI 7) (Figure 3(A)).¹⁹ The metagenomic investigation indicated that groundnut nodules harbour actinobacterium *Micromonospora*, which offers antibacterial characteristics and synthesizes secondary compounds that bolster the groundnut's defence mechanisms.⁵⁰ This indicates that root nodules function as microhabitats for diverse bacteria that enhance plant development, soil health, and nutrient availability.

The co-inoculation of RE with PE in groundnut resulted in an increased yield. Enhanced nodule quantities were noted in plants administered with *Rhizobium phaseoli* S18 and *Pantoea dispersa* YBB19B, as well as *Rhizobium mayense* S19 in conjunction with *Kosakonia oryzae* ESB1.¹⁹ The application of the groundnut endophytic bacterium *Bacillus firmus* J22N improved kernel and biomass yield. It enhanced plant development and bolstered the plant's resilience to salt stress by generating antioxidants and osmoprotectants.²⁷ The simultaneous inoculation of *Rhizobium pusense* S6R2, *Rhizobium phaseoli* S18, *Pantoea dispersa* YBB19B, *Bacillus altitudinis* TBB5A, and *Rhizobium pusense* S6R2 with *Bacillus tequilensis* NBB13 led to increased production of IAA and ACC deaminase, enhanced phosphorus solubilization, and improved nodule formation under saline conditions.²¹ The co-inoculation of *Bradyrhizobium* with rapidly proliferating *Klebsiella*, isolated from groundnut nodules, colonized the existing nodules and improved crop development.⁵¹ The seed treatment with non-rhizobial endophytic bacteria such as *Klebsiella pneumoniae* AG4, *Pseudomonas aeruginosa* ABG5, *Chryseobacterium indologenes* AM2, and *Enterobacter cloacae* ACP3, resulted in

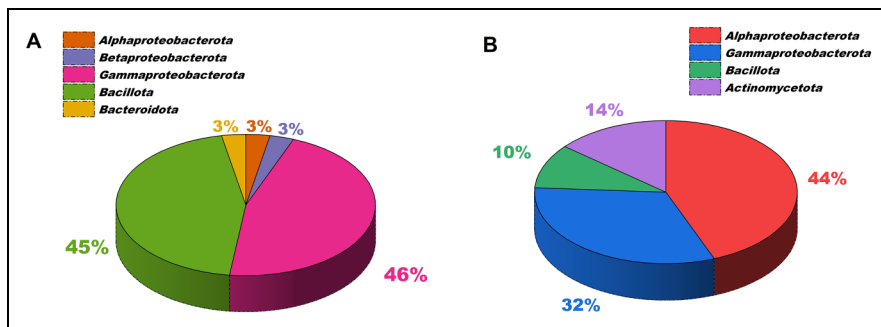


Figure 3. Comparative distribution of bacterial Phyla in groundnut nodules and phyllosphere. Section A represents the composition of nodule endophytes (Preyanga et al.¹⁹), while Section B depicts the microbial community in the phyllosphere (Krishnamoorthy et al.²⁹).

increased nitrogen fixation, phosphorus solubilization, siderophore synthesis, and ACC deaminase activity.⁵² Bacterial isolates such as *Bacillus* sp. GL2 and *Paenibacillus glycanilyticus* YMR3, inhabit the root tips of groundnut seedlings endophytically, enhancing groundnut biomass yield, nodule quantity, and jasmonic acid levels, thereby bolstering plant defence against pathogens.⁵³

Phyllospheric bacteria

The leaf surface, known as the phyllosphere, hosts a unique microbial community. These encompass microorganisms that enhance plant health, growth, and stress resilience, including bacteria and fungi. *Methylobacterium*, *Pseudomonas*, *Bacillus*, *Streptomyces*, *Aspergillus*, and *Trichoderma* are microorganisms present in the phyllosphere.⁵⁴ Eighty bacterial isolates of methylotrophs were obtained from fifteen groundnut genotypes. Among them, 29 were identified as pink-pigmented methylotrophs (PPFM), whereas 51 were classified as non-pink-pigmented methylotrophs. These methylotrophs represent phyla including *Alphaproteobacterota* (35), *Gammaproteobacterota* (26), *Bacillota* (8), and *Actinomycetota* (11) (Figure 3(B)). They safeguard plants from detrimental bacteria and fungi by synthesizing antibiotics.²⁹ These bacteria establish a competitive milieu for infections and impede their reproduction by colonizing the phyllosphere.⁵⁵ They enhance the plant's capacity to endure stress from salinity, drought, ultraviolet radiation, and nutrient deficiencies. Furthermore, several microorganisms produce antioxidants that protect plant cells from oxidative damage, including superoxide dismutase, peroxidase, and catalase.²⁷ Some phyllosphere microorganisms are known to synthesize plant growth-promoting substances like auxins, gibberellins, and cytokinins, which contribute to the enhancement of shoot and root development, as well as overall plant vigour.⁵⁶

The in vitro seed germination study, performed by inoculating methylotrophic bacteria isolated from the phyllosphere of groundnut genotypes, demonstrated that these isolates had various growth-promoting characteristics. Seed treatment with *Methylobacterium populi* TMV7-4, *Methylobacterium thiocyanatum* VRI7-A4, *Methylobacterium radiotolerans* VRI8-A4, *Pseudomonas psychrotolerans* ICGV-5, and *Pseudarthrobacter phenanthrenivorans* TMV7-A3 resulted in a greater quantity of root hairs, enhanced radicle length, increased shoot length, extended root length, and elevated dry weight.²⁹ Treating groundnut with *Bacillus firmis* GRS123, isolated from the rhizosphere, and *Bacillus megaterium* GPS 55 and *Pseudomonas aeruginosa* GPS21, both isolated from the phylloplane, resulted in a 26% increase in plant biomass.⁵⁷ The assessment of methylotrophs isolated from the groundnut phylloplane indicated that *Rhizobium pusense* TMV2-6 exhibited superior ACC deaminase activity, *Pseudomonas psychrotolerans* K-TMV7-6 demonstrated enhanced acetylene reduction assay activity, *Pantoea stewartii* subsp. *indologenes* N-CO6-5 generated elevated levels of IAA, and *Pantoea dispersa* ICGV-2 produced increased exopolysaccharide and solubilized phosphorus.⁵⁸ A significant improvement in seed germination was observed in a pot culture experiment with the phyllospheric *Methylorubrum aminovorans* PPFM-Tm13 encapsulated in polyvinyl alcohol nanofiber.⁵⁹

The neighbor-joining phylogenetic tree, constructed with MEGA7 software using 16S rRNA gene sequences of plant growth-promoting bacteria isolated from groundnut, classified these bacteria into the phyla *Pseudomonadota*, *Bacillota* (Gram-positive, Low G + C), *Actinomycetota* (Gram-positive, High G + C), and *Bacteroidota* including *Flavobacterium*.⁶⁰ Bacteria are classified within the *Pseudomonadota* phylum, including *Bradyrhizobium*, *Rhizobium*, and *Methylobacterium*, which are positioned distinctly in the phylogenetic tree. *Bradyrhizobium* established a distinct cluster independent from *Methylobacterium*. *Rhizobium* established a distinct clade apart from the cluster comprising *Bradyrhizobium* and *Methylobacterium*. *Betaproteobacterota* and *Gammaproteobacterota* constituted a distinct cluster apart from *Alphaproteobacterota*. *Actinomycetota* constituted a distinct group apart from the *Bacillota*. Additionally, *Bacteroidota* established a distinct and profound phylogenetic lineage from the other bacterial phyla (Figure 4).

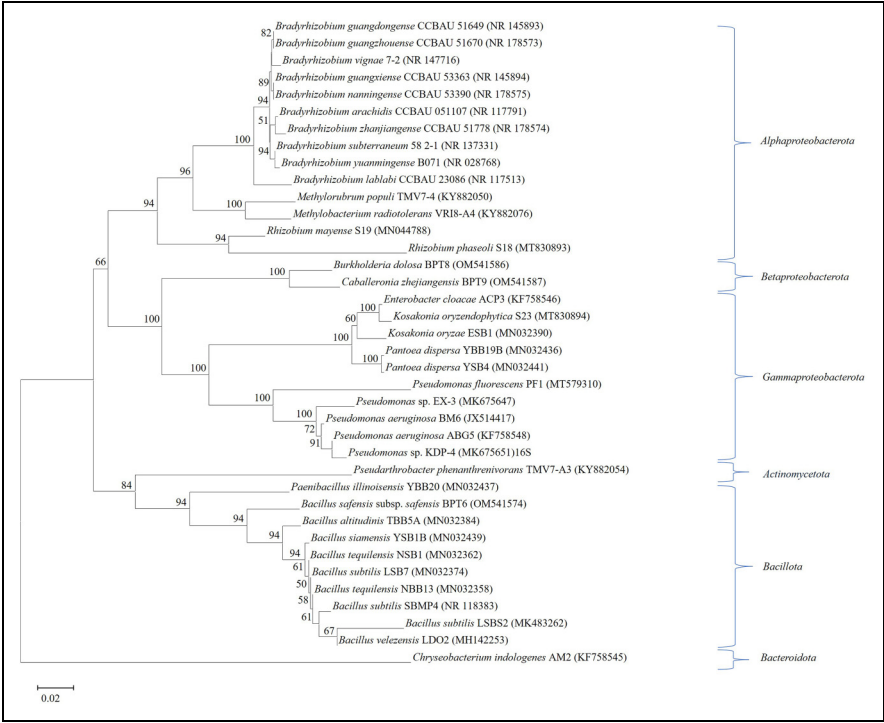


Figure 4. Phylogenetic relationships of plant growth-promoting Bacteria isolated from groundnut. Neighbour-joining phylogenetic tree based on 16S rRNA gene sequences of potential plant growth-promoting bacteria isolated from groundnut. Numbers at the nodes indicate bootstrap values, expressed as percentages of 1000 replications; only values >50% are shown. Bar, 0.02 changes per nucleotide position (Tamura et al.⁶⁰).

Endophytic fungi

Endophytic fungi inhabit the internal tissues of plants and derive advantages through direct and indirect methods, such as nutrient acquisition, synthesis of phytohormones, antibiotics, and siderophores, as well as the induction of resistance to diverse biotic and abiotic challenges.²⁸ Inoculation of endophytic fungus by immersion of groundnut seedlings in a *Phomopsis liquidambaris* B3 fungal suspension enhanced the chemotactic interaction of rhizobia with groundnut by altering the phenolic acids and flavonoids in root exudates. This interaction resulted in an increased number of nodules, enhanced nitrogen fixation efficiency, improved physiological parameters, and increased kernel yield in a monocropping system.⁶¹ A pot culture investigation on the co-inoculation of the endophytic fungal biocontrol agent *Trichoderma harzianum* and the nitrogen-fixing *Bradyrhizobium* sp. enhanced groundnut seed germination and increased biomass yield.⁶²

Mycorrhizal fungi

Mycorrhizal fungi serve as a significant bioinoculant for enhancing soil structure by producing extraradicular hyphae that facilitate macroaggregate formation. Arbuscular mycorrhizae, such as *Glomus mosseae*, synthesize a specific glycoprotein called glomalin, which functions as a binding agent, aggregating soil particles.^{63,64} Groundnut plants infected with *Glomus mosseae* exhibited improved growth due to higher nutrient absorption from the soil and increased production.⁶⁵ Arbuscular mycorrhizal fungi diminished the reliance on phosphorus fertilizers and enhanced phosphorus uptake by plants, resulting in higher nodulation and nitrogen fixation.⁶⁶ The utilization of commercial *Rhizobium* fertilizer in conjunction with AM fungus taxa such as *Glomus*, *Gigaspora*, and *Acaulospora* facilitated a tripartite symbiotic relationship with groundnut, enhancing plant development and yield.⁶⁷ The integration of Ca^{2+} with arbuscular mycorrhizae modifies the groundnut rhizosphere microbiota and enhances soil enzyme activity in conditions of salt stress. The populations of the phyla *Pseudomonadota* and *Bacillota*, as well as the *Sphingomonas* sp., increased following the application of mycorrhizal fungi.⁶⁸

Cyanobacteria for amelioration

Cyanobacteria, such as *Anabaena oryzae* and *Nostoc muscorum*, enhance nutrient uptake in groundnuts through nitrogen fixation, phosphate solubilization, potassium mobilization, calcium uptake, and IAA production. They fix atmospheric nitrogen via heterocysts, where nitrogenase converts N_2 into NH_3 , assimilated through the glutamine synthetase-glutamate oxaloacetate transaminase (GS-GOGAT) pathway. Phosphate solubilization occurs through the secretion of organic acids (gluconic, citric, and oxalic) and phosphatases, releasing bioavailable phosphorus for root absorption. Potassium mobilization involves acid-mediated weathering of K-bearing minerals, making K^+ ions available for uptake via root K transporters. Calcium solubilization is facilitated by organic acid

excretion and biofilm-induced pH modifications, enhancing Ca^{2+} absorption.⁶⁹ Additionally, cyanobacteria produce IAA, promoting root elongation and lateral root formation, and increasing nutrient uptake efficiency. These mechanisms collectively improve soil fertility, plant growth, and stress resilience, reducing dependence on chemical fertilizers and supporting sustainable groundnut cultivation.⁷⁰

Mechanisms of growth promotion of groundnut by plant growth-promoting bacteria

The diverse microbial communities associated with groundnut, spanning rhizosphere, endophyte, and phyllosphere niches, play a pivotal role in improving soil health, nutrient availability, and plant resilience. These microorganisms contribute not only by fixing nitrogen, solubilizing phosphorus, and mobilizing essential minerals but also by modulating plant hormone levels, producing bioactive compounds, and enhancing systemic resistance against biotic and abiotic stresses. Understanding the specific mechanisms by which plant growth-promoting microorganisms (PGPM) exert their beneficial effects is crucial for harnessing their full potential and helps optimize microbial inoculants in sustainable groundnut cultivation. The interactions between groundnut and beneficial microorganisms are dynamic, involving multiple direct and indirect pathways that collectively support plant growth, enhance stress tolerance, and suppress pathogens.⁷¹ The growth-promoting characteristics of prospective microorganisms linked to groundnut are listed in Table 2.

Table 2. Plant growth promoting traits of the potential of microorganisms associated with groundnut.

Bioinoculants	Function	Reference
<i>Rhizobium</i> sp.	Symbiotic N fixation	72
<i>Bradyrhizobium</i> sp.		73
<i>Methylobacterium</i> sp.	Induced systemic resistance activity against rot pathogen	55
<i>Pantoea dispersa</i>	P solubilization	58
<i>Thiobacillus</i>	Increased yield in soils deficient in sulphur	74
<i>Glomus mosseae</i>	Increased nutrient uptake	65
<i>Glomus intraradices</i>	Augmented growth parameters, biochemical makeup, and nutrient content	75
<i>Bacillus firmus</i>	Increased plant tolerance to salt stress	27
<i>Sphingomonas</i> sp.		76
<i>Microcoleus</i> sp.	Growth promotion under drought stress	77
<i>Bacillus amyloliquefaciens</i>		78
<i>Azospirillum brasilense</i>	Promoted the development of primary root	79
<i>Trichoderma harzianum</i>	Reduces seed contamination by aflatoxin produced by <i>Aspergillus</i> sp.	80
<i>Kocuria turfanensis</i>	IAA production	

Direct mechanisms

Nitrogen fixation. Biological nitrogen fixation is an energy-dependent process that consumes 16 ATP molecules and 8 hydrogen molecules, converting di-nitrogen into two ammonia molecules. In a symbiotic relationship, plants provide 12 g of carbon source (glucose) to bacteria for each gram of nitrogen fixed.⁸¹ The inoculation of *Rhizobium* in groundnuts promotes plant development, augments production, and sustainably boosts soil health.⁷² *Rhizobium* fixes 112–152 kg of nitrogen per acre annually in groundnut.⁸² *Bradyrhizobium* sp. was identified as the predominant nitrogen-fixing bacterium in groundnut, promoting growth and yield.²⁶ The application of *Bradyrhizobium* and *Trichoderma harzianum*, each at 2 g/kg of seeds, in conjunction with gypsum and the prescribed fertilizer dosage, resulted in increased production in groundnut.⁸³ Biochar enhances soil fertility, sequesters significant quantities of carbon, and contributes to climate change mitigation. A study on utilizing rice husk char as a carrier material for the soil application of *Rhizobium* demonstrated enhancements in soil nitrification, improved nodule formation and yield, and carbon sequestration, consequently mitigating greenhouse gas emissions.⁸⁴ The application of a consortium of bacterial biofertilizers, including *Azospirillum*, *Azotobacter*, *Rhizobium*, and phosphobacteria, in conjunction with AM fungus, enhanced the biochemical parameters such as chlorophyll and protein content in groundnut kernels.⁸⁵

Nodule formation by *Rhizobium* sp. in groundnut. Most studies in groundnuts demonstrated that the root nodules are majorly formed by the slow-growing *Bradyrhizobium* sp. and scarcely by the fast-growing *Rhizobium* sp. The rhizobial isolates, *Rhizobium huautlense* BN 20, *Rhizobium pusense* BN 23, and *Rhizobium alikisoli* BN 50 were found to nodulate groundnut and promote plant growth under stressed conditions.⁸⁶ Nitrogen fixation by *Rhizobium* encompasses multiple steps, beginning with plant signaling and culminating in the formation of nitrogen-fixing nodules (Figure 5). The roots of legumes exude flavonoids into the soil, which attract *Rhizobium* for infection. This bacterium adheres to the root hair surface through the mediation of a plant protein known as lectin. Following infection, the bacterial transcriptional regulator protein (NodD) was activated, which stimulates the transcription of nodulation genes, resulting in the production of Nod factors (signalling molecules known as lipo-chito oligosaccharides [LCOs]). Nod factors are responsible for the production of nodules in leguminous plants. Upon Nod factors initiation, the root hairs undergo deformation and curling, creating a structure that encapsulates *Rhizobium*. At this stage, infection threads are established, enabling the bacterium to infiltrate the cortical region, where *Rhizobium* cells are liberated from the infection threads into individual root cells. They transform into specialized forms known as bacterioids, which can convert atmospheric nitrogen into ammonia. These structures are encased by plant membranes that create an optimal environment for *Rhizobium* development. These bacterioids develop and form root nodules.⁸⁷

Nodulation by *Bradyrhizobium* sp. in groundnut. *Bradyrhizobium* sp. is chemotactically drawn to groundnut root hairs by flavonoids (daidzein, genistein, and chrysin) exuded by

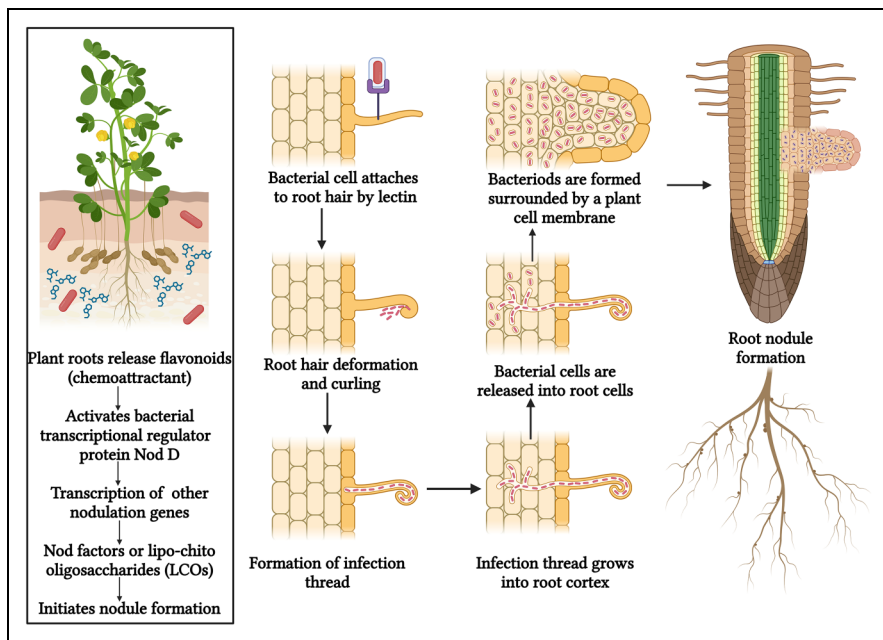


Figure 5. Mechanism of *Rhizobium* nodulation in groundnut through root hair entry. The sequential process of root nodule formation in groundnut through symbiotic interaction with *Rhizobium*. The process begins with the release of flavonoids from plant roots, which act as chemoattractants, activating the bacterial transcriptional regulator protein NodD. This activation leads to the transcription of nodulation genes and the production of Nod factors (lipo-chito oligosaccharides), which initiate nodule formation. *Rhizobium* cells then attach to root hairs through lectin, triggering root hair deformation and curling. This structural change facilitates the formation of an infection thread, which extends into the root cortex, allowing bacterial cells to be released into plant cells. Inside the developing nodule, *rhizobia* differentiate into nitrogen-fixing bacteroids, surrounded by a plant-derived membrane (Yang et al.⁸⁷). This ultimately results in the formation of mature root nodules, which play a crucial role in enhancing biological nitrogen fixation and promoting plant growth.

the plants. The typical mechanism for rhizobial entry into groundnut involves intercellular penetration through cracks in the root and cortex, leading to the formation of an infection thread.⁸⁸ *Bradyrhizobium* infiltrates the root via the intermediate lamella between neighbouring axillary hair cells and infects substantial basal cells linked to certain axillary root hairs, resulting in the formation of determinate nodules.⁸⁹ The development of nodules in legumes by nitrogen-fixing *Bradyrhizobium* entails several stages. The bacterium located at the lateral roots adjacent to the axillary root hairs infects the roots of legumes. Upon entering the roots, the bacterium disseminates between the plant cells and infiltrates the interior tissues of the roots. In the root cortical region, they initiate proliferation and develop nodule primordia (precursors of root nodules). As bacterial cells grow, plant cells experience morphological alterations and develop immature nodules

that subsequently mature into fully developed bacteroids, which are structures that fix atmospheric nitrogen (Figure 6).⁹⁰

Phosphate solubilization. The utilization of phosphate solubilizing bacteria as biofertilizers transforms insoluble phosphorus into a soluble form via mechanisms such as soil pH reduction through organic acid production and H^+ release, cation chelation, and organic phosphorus mineralization, thereby enhancing phosphorus uptake by plants.⁹¹ Inoculating groundnut with *Bacillus thuringiensis* B1 in acidic soils enhanced phosphate availability and protein yield.⁹² *Providencia rettgeri* TPM23 is a prospective plant growth-promoting bacterium isolated from encrusted environmental surface soils with significant phosphate solubilization capability, which mitigates the impact of salt stress in groundnut.⁹³ *Acinetobacter pittii* YMX11, *Pseudomonas indica* TPMX14, *Brevibacillus shisleri* TPMX3, *Chryseobacterium lathyr* YMX8, *Paenibacillus illinoisensis* TMX9, *Gordonia terrae* TPMX16, and *Ensifer sesbaniae* TPMX5 isolated from groundnut rhizosphere are recognized for their salt-tolerant phosphate solubilizing capabilities, making them potential bioinoculants for groundnut to promote plant growth under saline conditions.⁹⁴

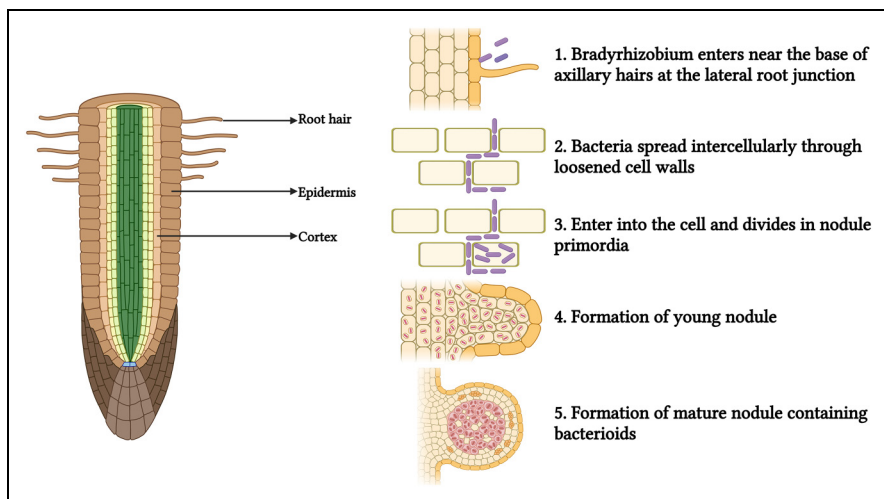


Figure 6. Mechanism of *Bradyrhizobium* nodulation in groundnut through crack entry. The process of root nodule formation in groundnut through the crack entry mechanism facilitated by *Bradyrhizobium*. The process begins when *Bradyrhizobium* enters near the base of axillary root hairs at the lateral root junction. The bacteria then spread intercellularly through loosened cell walls, creating a pathway for colonization. Once inside, the bacterial cells enter plant cells and undergo division within the nodule primordia, leading to the initiation of nodule formation. As the process progresses, young nodules develop and mature into fully functional nodules containing differentiated bacteroids (Sharma et al.⁹⁰). These bacteroids play a crucial role in biological nitrogen fixation, enhancing the plant's ability to acquire atmospheric nitrogen and promoting overall growth and productivity.

Serratia sp. S119, isolated from groundnut nodules, solubilizes inorganic phosphates via gluconic acid synthesis, also synthesizes the phytohormone IAA, and inhibits the growth of the pathogen *Sclerotinia sclerotiorum*, responsible for sclerotinia rot or stem rot.⁹⁵ The phosphate-solubilizing rhizospheric bacteria *Bacillus subtilis*, isolated from groundnut, may serve as a promising bioinoculant.⁹⁶ The assessment of the prolonged impacts of inoculating the phosphate-solubilizing bacterium *Burkholderia cepacia* ISOP5 and the photosynthetic purple non-sulphur bacterium *Rhodopseudomonas palustris* ISP-1 as biofertilizers for groundnut demonstrated an enhancement in seed protein content and an increased relative abundance of genes associated with nitrogen metabolism.⁹⁷

Potassium solubilization. Potassium solubilizing bacteria typically employ mechanisms such as pH reduction, chelation, and acidolysis.⁹⁸ Potassium-solubilizing *Micrococcus varians* and *Corynebacterium kutscheri*, when applied to groundnuts, were observed to enhance the quantity of pods and seeds per plant.⁹⁹ The pot culture experiment on groundnut utilizing *Bacillus* sp. PG10, isolated from the rhizosphere of pearl millet, demonstrated superior potassium solubilization capacity, increased seed germination, and enhanced morphological characteristics.¹⁰⁰

Sulphur oxidation. Sulphur oxidizers convert reduced forms of sulphur such as sulphides, thiosulphates, and elemental sulphur into sulphate making it available to plants. Pot culture and field trials including the simultaneous administration of *Thiobacillus* sp. LCH (an autotrophic sulphur-oxidizing bacterium) and *Rhizobium* TNAU14 in the groundnut variety ALR 2 increased both nodule quantity and nodule dry weight.⁷⁴ Co-inoculation of *Rhizobium* with sulphur-oxidizing bacteria, namely *Thiobacillus* strains, in field settings characterized by sulphur-deficient soils resulted in enhanced nodulation, higher plant biomass, elevated accessible sulphur in the soil, an 18% augmentation in pod yield, and improved oil content.⁷⁴ Groundnut seeds inoculated with sulphur-oxidizing bacteria and *Rhizobium*, along with gypsum application to the soil, augmented the available sulphur and improved yield.¹⁰¹

Phytohormone production. Microorganisms that promote plant growth synthesize phytohormones like auxin (indole-3-acetic acid), cytokinin, gibberellins, ethylene suppressor (1-aminocyclopropane-1-carboxylate deaminase), and abscisic acid.¹⁰² Pot and field trials including the inoculation of pseudomonads from the groundnut rhizosphere have demonstrated the production of IAA and siderophores, the solubilization of inorganic phosphate, inhibition of *Aspergillus niger*, *Aspergillus flavus*, and *Sclerotium rolfsii*, as well as the enhancement of plant growth and yield.¹⁰³

Siderophore production. Siderophores are low molecular weight (200–2000 Da), high-affinity iron-chelating compounds synthesized in iron-deficient environments. They solubilize Fe^{3+} for absorption, replace detrimental pesticides, detoxify heavy metal pollutants, and serve as potential biocontrol agents and biosensors. Siderophore-producing bacteria encompass *Pseudomonas fluorescens* (ferribactin), *Trichoderma* sp. (coprogen),

Fusarium sp. (fusigen), *Klebsiella pneumoniae* (enterochelin), *Streptomyces pilosus* (Desferrioxamine B), *Bacillus subtilis* (bacillibactin), and *Rhizobium meliloti* (rhizobactin).^{104,105} The field inoculation of the catecholate-type siderophore bacillibactin and *Bacillus subtilis* LSBS2 enhanced iron chelation, oil content, total biomass, and improved plant immunity.¹⁰⁶ The chelation of iron by the siderophores inhibited the growth of plant pathogens indirectly by making iron unavailable to them.¹⁰⁷ A study on the dihydroxamate type of siderophore produced by the *Rhizobium* isolates namely RM-1, RM-2, and RM-3 from groundnut rhizosphere exhibited antifungal activity against the collar rot pathogen *Sclerotium rolfsii*.¹⁰⁸

Indirect mechanisms

Microbial inoculants in disease suppression in groundnut. Microbial inoculants act as biocontrol agents for plant pathogens, enhancing crop production and protection, ensuring sustainability, and food safety, and reducing the need for toxic chemicals.¹⁰⁹ The talc-based formulation of the biofertilizer *Azospirillum brasilense* Az 204 and the biocontrol agent *Pseudomonas fluorescens* strain PF1, applied to soil in groundnut cultivation, improved root and shoot growth.⁷⁸ *Pseudomonas aeruginosa* AMAAS 57, which produces 2,4-diacetylphloroglucinol (2,4-DAPG), was isolated from the groundnut rhizosphere and demonstrated efficacy in suppressing soil pathogens, specifically *Sclerotium rolfsii* and *Aspergillus niger*, responsible for stem rot and collar rot, respectively.¹¹⁰ A pot culture experiment showed that the simultaneous inoculation of AM fungus (*Glomus fasciculatum*) and the biocontrol agent (*Trichoderma viride*) significantly reduced *Sclerotium rolfsii* in groundnut and enhanced plant growth.¹¹¹

Induction of systemic resistance. Plant growth-promoting microorganisms (*Rhizobium* sp., *Glomus* sp., *Trichoderma* sp., *Pseudomonas* sp., and *Bacillus* sp.) indirectly induced systemic resistance in plants. They activate the plant's defensive mechanisms against diverse diseases upon exposure to specific triggers. Induced systemic resistance (ISR) is facilitated by the jasmonic acid or ethylene signalling pathways, resulting in enhanced plant health and productivity. The ISR response in plants entails the activation of certain defence genes, and the synthesis of pathogenesis-related proteins (PR proteins), phytoalexins, phenolics, and exopolysaccharides that directly impede pathogens.¹¹² Microbial elicitors such as lipopolysaccharides, terpenoids, and flagellin stimulate defensive mechanisms against infections.¹¹³ *Pseudomonas aeruginosa* RP2, when colonizing groundnut, demonstrated an induced defence response by inhibiting the stem rot pathogen, *Sclerotium rolfsii*, via the root exudate metabolites benzoic acid and salicylic acid.¹¹⁴ A study on groundnut treatment using *Methylobacterium* sp. PPFM-Ah with challenge inoculation of pathogenic *Aspergillus niger* or *Sclerotium rolfsii* demonstrated enhanced activity of peroxidase (PO), phenylalanine ammonia-lyase (PAL), and β -1,3-glucanase, which elicited systemic resistance against rot pathogens.⁵⁵ The seed treatment with *Methylobacterium radiotolerans* VRI8 A4 in groundnut elicited induced systemic resistance (ISR) against seed-borne fungal infections.¹¹⁵

Antibiosis. Microbial inoculants produce some bioactive compounds which inhibit the plant pathogens, supporting plant health. *Bacillus velezensis* LDO2, an endophytic bacterium from groundnut, synthesizes a range of antifungal and antibacterial compounds, including bacilysin, butirosin, bacillaene, difficidin, fengycin, macrolactin, and surfactin, which inhibit plant diseases and enhance plant growth.¹¹⁶ *In vitro*, research on *Pseudomonas aeruginosa* P4, which colonizes the groundnut rhizosphere, demonstrated the production of the antibiotic pyocyanin, which exhibits antibiosis against *Fusarium oxysporum*.¹¹⁷

Hydrolytic enzymes. Hydrolytic enzymes such as chitinase, glucanase, protease, and cellulase produced by microbial inoculants can degrade the cell walls of plant pathogens. The enzyme α -1,4-N-acetylglucosaminidase derived from *Bacillus subtilis* AF1 isolated from the pigeon pea rhizosphere region inhibited the germination of urediniospores of the rust pathogen *Puccinia arachidis*.¹¹⁸ *Pseudomonas aeruginosa* strain Kasamber 11, *Bacillus subtilis* SBMP4, and *Pseudomonas aeruginosa* A1K319 isolated from iron-deficient rhizospheric soil exhibited elevated production of hydrolytic enzymes cellulase, pectinase, and chitinase.¹¹⁹

Beyond enhancing nutrient availability and plant growth, microbial inoculants play a crucial role in improving crop quality. Their ability to influence key physiological and biochemical processes translates into better yield, higher nutrient content, and improved produce quality. In groundnut, the application of beneficial microbes such as *Rhizobium*, phosphate-solubilizing bacteria, and arbuscular mycorrhizal fungi has been shown to enhance kernel yield, oil content, and protein levels. Let's explore how these microbial inoculants contribute to both the productivity and quality of groundnut.

Combined effect of microbial inoculants and other treatments on groundnut growth, yield, and quality parameters

Microbe-based bioinoculants play a crucial role in the growth and development of groundnut from seed germination to the pod development stage. It significantly enhances the quality indices of groundnut, including pod yield, protein, and oil content. The groundnut production is augmented by 65% with the synergistic application of *Rhizobium* and phosphorus fertilizer.¹²⁰ A study examining the impact of quality parameters of groundnut, utilizing zinc solubilizing bacteria and liquid formulations of recommended NPK fertilizer doses, yielded increased kernel yield, haulm yield, and an enhancement of 6.7 kg of oil per hectare, along with an approximate increase of 4.4 kg in protein content per hectare.¹²¹ A pot culture experiment utilizing the synergistic application of biofertilizers, comprising phosphate solubilizing bacteria and arbuscular mycorrhizal fungus, alongside homo-brassinolide, which modulates phytohormones, yielded a 30% rise in kernel production and a 45% enhancement in oil content.¹²² Inoculation with *Rhizobium* resulted in a maximum oil content of around 46% in the kernels.¹²³ Field experiments demonstrated a groundnut kernel yield of 2173 kg per hectare, accompanied by a shelling percentage of 79%, achieved through the application of a prescribed dosage of phosphatic fertilizer, phosphate solubilizing bacteria,

arbuscular mycorrhizal fungi, and farmyard manure.¹²⁴ The co-inoculation of PGPR *Stenotrophomonas maltophilia* BJ01 facilitated groundnut growth by increasing the synthesis of auxin, phenolic compounds, flavonoids, antioxidant levels, and osmoprotectants in nitrogen-deficient conditions. A field experiment conducted with nitrogen treatment in conjunction with *Rhizobium* and phosphobacteria demonstrated enhanced growth and yield characteristics, achieving a kernel yield of 2656 kg/ha.¹²⁵ The application of *Rhizobium* and *Pseudomonas striata* for seed treatment in groundnut enhanced the yields of dry pods and haulm. Furthermore, it led to an augmentation of microbial populations and organic carbon levels in the post-harvest soil.¹²⁶ The application of a liquid formulation of zinc-solubilizing bacteria combined with NPK in groundnut enhanced crop physiology, yielding a kernel output of 2114 kg/ha.¹²¹ The administration of a 100% recommended dose of phosphorus (RDP) combined with Farm Yard Manure, phosphate solubilizing bacteria, and arbuscular mycorrhizae resulted in the greatest shelling percentage of 79.23% and a test weight of 42.22 g in groundnut, surpassing the application of 100% RDP alone.¹²⁴ The utilization of indigenous strains of sulphur-oxidizing bacteria (*Pseudomonas aeruginosa* AAU PF 3 and *Bacillus tropicus* AAU SOB 1) and a zinc-solubilizing bacterium (*Beijerinckia fluminensis* AAU ZSB F2) in groundnut, combined with a prescribed dosage of fertilizers, gypsum, and zinc sulphate, enhanced the oil content by 53% and protein content by 31.82% in the kernel.¹²⁷ The application of liquid bioinoculants including N-fixing *Bradyrhizobium*, and the zinc solubilizing bacterium, *Pseudomonas striata*, resulted in the maximum dry pod yield of 29.10 quintals per hectare.¹²⁸ The application of *Aspergillus terreus*, a zinc-solubilizing fungus, at a dosage of 2.5 litres per hectare alongside 100% recommended dose of fertilizers (RDF) yielded superior pod (14.96 g) and haulm (20.18 g) production per plant.¹²⁹ The combined application of phosphorus (60 kg P₂O₅/ha) and *Rhizobium* inoculant (6 g /kg of seed) resulted in an average yield of 2812.5 kg/ha with a benefit-cost ratio of 3.¹³⁰ The P fertilizer input was reduced by 15 kg from the recommended RDF (75 kg) with the use of microbial inoculants.

In addition to enhancing the yield and quality of groundnut, microbial inoculants contribute to overall plant health by improving soil fertility and microbial diversity. Their beneficial effects extend beyond nutrient enrichment, as they also help plants withstand various environmental stresses. This resilience is particularly crucial in the face of abiotic stresses, which can severely limit groundnut productivity.

Microbial inoculants in the alleviation of abiotic stresses in groundnut

Among the various abiotic stresses, soil salinity and drought pose significant challenges to groundnut cultivation, affecting plant metabolism, nutrient uptake, and overall yield.

Salt stress

Soil salinity, among other abiotic stimuli, adversely impacts plant growth and development while contributing to land degradation¹³¹. Research conducted to investigate the

impact of salt stress on groundnuts demonstrated that soil salinity modifies the rhizosphere bacteria. The genera *Sphingomonas* and *Microcoleus* predominated in salt-affected soils, exhibiting elevated metabolic activities that aid plants in enduring salt stress via several processes including signalling.¹³² The phyla *Cyanobacteriota* and *Pseudomonadota* exhibited an increase, while *Acidobacteriota* demonstrated a decline following salt treatment.⁷⁶ Research on bacterial genera inhabiting the spermosphere of groundnut identified *Bacillus*, *Massilia*, *Pseudarthrobacter*, and *Sphingomonas*. The genus *Bacillus* exhibited increased phosphatase activity, which facilitated phosphorus absorption and improved germination under saline stress.¹³³ Pot culture experiments on groundnut using PGPR strains *Pseudomonas aeruginosa* AMAAS57 and *Pseudomonas aeruginosa* BM6 resulted in enhanced production of phenols and amino acids, which help mitigate free radicals and act as osmolytes under salt stress, respectively.¹³⁴ Gas chromatography-mass spectrometry (GC-MS) metabolomics and metagenomic research indicated that intercropping groundnut with sorghum enhanced salt stress resistance through the regulation of root metabolites and the presence of beneficial microbes.¹³⁵ A study on inoculation of halotolerant rhizobacterial strains (*Klebsiella* sp. MBE02, *Pseudomonas* sp. MBE05, *Agrobacterium tumefaciens* MBE01, and *Ochrobactrum anthropic* MBE03) isolated from halophyte *Arthrocnemum indicum* in groundnut exhibited N fixation, P solubilization, ACC deaminase production reducing ethylene levels by breaking down ACC (precursor of ethylene) into α -ketobutyrate and ammonia, ion homeostasis, and oxidative stress mitigation under salt stress.¹³⁶ The inoculation of arbuscular mycorrhizal fungi increased the abundance of the bacterial phyla *Pseudomonadota* and *Bacillota*, as well as the fungal taxa *Ascomycota* and *Haematonectria*. This led to enhanced groundnut yield in saline-alkali soils.¹³⁷ Plant-promoting fungi (PGPF), specifically *Trichoderma asperellum* and *Trichoderma virens*, enhanced plant development during the vegetative phases of groundnut under salinity stress.¹³⁸ The treatment of endophytes (*Bacillus firmus* J22N; *Bacillus tequilensis* SEN15N; and *Bacillus* sp. REN51N) in groundnut led to increased pod yield under salt stress by producing ROS scavenging enzymes, ACC deaminase, and accumulating proline.²⁷ The simultaneous inoculation of *Rhizobium pusense* S6R2, *Rhizobium phaseoli* S18, *Pantoea dispersa* YBB19B, *Bacillus altitudinis* TBB5A, *Rhizobium pusense* S6R2 and *Bacillus tequilensis* NBB13 resulted in enhanced IAA and ACC deaminase production, increased phosphorus solubilization, and improved nodule formation under saline stress conditions.²¹ *Enterobacter cloacae* S23, an endophytic passenger in groundnut, acquired elevated levels of proline during saline stress.¹³⁹

Drought stress

The populations of *Actinomycetota*, *Acidobacteriota*, *Cyanobacteriota*, and *Gemmatimonadota* proliferated in the groundnut rhizosphere under drought stress, enhancing the drought tolerance of groundnut.⁴³ The inoculation of the endophytic fungus *Phomopsis liquidambaris* B3 enhanced the colonization of root-associated AM fungi, particularly *Gigaspora margarita*, and conferred drought resistance.¹⁴⁰ Drought-resistant *Pseudomonas* isolated from the groundnut rhizosphere produces ACC deaminase and

exopolysaccharides, reducing ethylene generation, improving water retention, and promoting root growth under drought stress.¹⁴¹ *Pseudomonas* strain PCKR-2, isolated from the groundnut rhizosphere, had the highest phosphorus solubilization index and improved plant development under drought conditions.¹⁴² The consortium of *Agrobacterium deltaense* AMT1, *Caballeronia zhejiangensis* BPT9, *Burkholderia dolosa* BPT8, and *Bacillus safensis* BPT6 improved plant growth and augmented kernel and oil yield under drought conditions.¹⁴³ The endophytic drought-tolerant bacterium *Bacillus amiloliquefaciens* TG4 (Pj2), isolated from the roots of *Prosopis juliflora*, demonstrated many plant growth-promoting properties in groundnut when inoculated under drought stress conditions.⁷⁷ The endophytic bacteria *Rhizobium pusense* S6R2, *Enterobacter cloacae* S23, *Rhizobium phaseoli* S10R2, *Bacillus altitudinus* TBB5A, and *Rhizobium mayense* S11R2 serve as effective bioinoculants for groundnut to mitigate drought stress which accumulates a significant amount of osmolytes such as proline, trehalose, and glycine betaine causing osmolyte adjustment, scavenge free radicals, maintain membrane integrity.¹⁴⁴

The role of microbial inoculants in alleviating abiotic stresses in groundnuts extends beyond direct plant growth promotion and stress mitigation. These beneficial microbes influence key physiological and biochemical pathways, leading to osmolyte accumulation, oxidative stress reduction, improved nutrient uptake, and enhanced microbial interactions in the rhizosphere. A crucial aspect of this interaction is the modulation of root exudate composition. Microbial inoculation influences metabolite profiles in root exudates, which in turn shape plant–microbe interactions under stress conditions. Understanding these changes in metabolite profiles provides insights into how microbial inoculants indirectly contribute to stress tolerance, thereby establishing a mechanistic link between abiotic stress alleviation and root exudate modifications.

Effect of microbial inoculants in root exudate metabolites

Root exudates serve as a primary interface between plants and soil microbiota, influencing microbial colonization, nutrient cycling, and stress responses. The composition of root exudates is dynamic and significantly modulated by microbial inoculants, particularly under abiotic stress conditions. Beneficial microbes alter the secretion of organic acids, amino acids, phenolics, and secondary metabolites, thereby enhancing nutrient availability and stress resilience in groundnuts. Understanding the interplay between microbial inoculants and root exudate metabolites provides insights into optimizing plant–microbe interactions for sustainable stress management in groundnut cultivation. Microbial inoculants influence root exudate metabolites, enhancing stress resilience in groundnuts through microbial interactions and biochemical defence mechanisms.

Previous research indicated that the co-inoculation of rhizobial endophytes (RE) *Rhizobium phaseoli* S18, *Rhizobium pusense* S6R2, *Rhizobium pusense* S6R2 with passenger endophytes (PE) *Pantoea dispersa* YBB19B, *Bacillus tequilensis* NBB13, *Enterobacter cloacae* S23 and *Pseudomonas aeruginosa* RP2 in groundnut resulted in modifications to root exudate metabolites under saline and drought-stressed conditions.^{19–21} These metabolites exhibit antibacterial, antiviral, antioxidant, and

insect-repellent activities, enhancing plant defence and abiotic stress tolerance (Table 3, Figure 7). After endophytic bacterial colonization, groundnut plants produce a variety of signalling molecules like 2,4-di-tert-butylphenol, 1-nonadecene, and nonadecanol which help to attract beneficial microorganisms. Metabolites such as 1-tridecene, hexadecenoic acid, 1-hexadecanol, cyclotetracosane, and pentatriacontane possess antimicrobial properties and act as natural defence mechanisms against soil-borne pathogens. Root exudate metabolites such as quassin, and epoxylanostan are produced in response to drought and saline stress to assist plants in coping with the stress by modifying microbial community and promoting beneficial interactions but their precise molecular functions require further exploration.

Molecular docking of root exudate metabolites produced from rhizobial and passenger endophytes with stress-responsive protein under saline and drought stress conditions

Molecular docking serves as a powerful tool to explore ligand–protein interactions, providing insights into how root exudate metabolites influence stress-responsive pathways at the molecular level. By docking metabolites from microbial-inoculated groundnut root exudates with key stress-related proteins such as DREB, Syntaxin, VIT1, and LEA, we can predict their binding affinities and potential roles in enhancing plant tolerance to salinity and drought stress. These computational analyses help bridge the gap between biochemical metabolite profiling and functional stress adaptation, offering promising leads for enhancing abiotic stress resilience in groundnuts.

Recent studies indicate that molecular docking is an essential method for elucidating interactions between ligands and receptors.¹⁴⁵ Molecular docking approaches have been utilized to predict probable interactions between small compounds and diverse plant target proteins.¹⁴⁶ This study utilized the compounds from root exudates produced by the co-inoculation of rhizobial and passenger endophytes under saline and drought stress conditions and docked them with four previously identified stress proteins.^{19–21}

Dehydration-responsive element-binding (DREB) proteins are crucial for regulating plant responses to abiotic stressors, including salt. DREB proteins play a crucial role in identifying and attaching to particular DNA sequences in the promoter regions of stress-responsive genes, known as DRE/CRT motifs (dehydration-responsive element/C-repeat).¹⁴⁷ Moreover, the Syntaxin protein significantly influences plant development and stress responses in *Arabidopsis* by modulating cell wall formation, pH levels, and reactive oxygen species (ROS) levels.¹⁴⁸ The VIT1 protein is essential for iron homeostasis in plants during drought conditions. It contributes to drought resistance by positively interacting with tetracyclic diterpenoids, which mitigate oxidative stress during water scarcity.¹⁴⁹ The LEA protein is essential for plant drought survival by stabilizing cellular structure, regulating ion and osmotic equilibrium, and mitigating oxidative damage by lowering reactive oxygen species in plant cells.¹⁵⁰ All proteins were modelled utilizing SWISS-MODEL in the current investigation (Figure 8(A) and (B)). Flexible loops were adjusted in restricted regions of the protein structure. The Computed Atlas of

Table 3. Functional properties of root exudates under different inoculation and stress conditions in groundnut.

Metabolites	Functions	References
Uninoculated control		
1-Tridecene	Antimicrobial property, pathogen suppression	19
2,4-di-tert-butylphenol	Antioxidant property, microbial signalling	
Pentatriacontane	Antimicrobial and antioxidant properties	
Eicosane	Plant defense	
1-Nonadecene	Signalling molecule, antimicrobial property	
Cyclononasiloxane	Signalling molecule	
RE and PE inoculated		
2,4-Di-tert-butylphenol	Antioxidant property, microbial signalling	19
1-Nonadecene	Signalling molecule, antimicrobial property	
11-Methyltricosane	Plant defence, attractant of beneficial insects and pollinators	
1-Tridecene	Antimicrobial property, pathogen suppression	
Eicosane	Plant defense	
Phenol	Antimicrobial activity, stress response	
Nonadecanol	Antimicrobial properties, chemical signalling	
Tetracosane	Suppression of pathogens	
Triacetyl heptafluorobutyrate	Plant defense	
Dotriacontane	Microbial interaction, stress response	
<i>Pseudomonas aeruginosa</i> RP2 inoculated		
Benzoic acid	Antifungal metabolite	114
Salicylic acid	Antifungal and signalling molecule	
Moisture-stressed condition (uninoculated control)		
Hexadecanoic acid	Antimicrobial property, drought stress response	144
Octadecenoic acid	Suppress-borne pathogens and triggers ABA leading to stomatal closure in plants (drought stress response)	
Fumaric acid	Antioxidants, maintain turgor pressure under saline stress	
1-Nonadecene	Signalling molecule, antimicrobial property	
1,2- Benzenedicarboxylic acid	Stress response	
Trans-13-octadecenoic acid	Signalling molecule	
Moisture-stressed condition (inoculated with RE and PE)		
Hexadecanoic acid	Antimicrobial property, drought stress response	144
Octadecenoic acid	Suppress-borne pathogens and triggers ABA leading to stomatal closure in plants (drought stress response)	
Octadecene	Form hydrophobic barrier in roots (water retention), signal for stress response	
Acetic acid	Activation of ABA increases nutrient uptake by solubilization	
Quassin	Antimicrobial property, insecticidal and nematicidal effect, stress response	

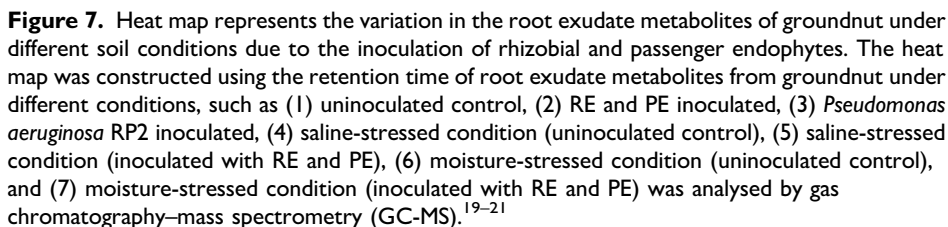
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Table 3. Continued.

Metabolites	Functions	References
I-Docosene	Insect repellent	
Deoxyspergualin	Antibiotic compound	
I-Hexadecanol	Antioxidant and antimicrobial properties	
Heptadecane	Antioxidant property	
Heptacosane	Stress signalling	
Fumaric acid	Antioxidants, maintain turgor pressure under stress conditions	
Saline-stressed condition (uninoculated control)		
Octacosanol	Antioxidant property	21
Cyclotetradecane	Antimicrobial property	
Hexadecanoic acid	Antimicrobial property	
Pentatriacontane	Antioxidant and antimicrobial properties	
I-Nonadecene	Signalling molecule, antimicrobial property	
I-Docosene	Insect repellent	
Docosanoic acid	Antimicrobial property	
Saline-stressed condition (inoculated with RE and PE)		
Octacosanol	Antioxidant property	21
Triacotane	Osmotic adjustment under stress	
Octacosane	Scavenge ROS	
Pentatriacontane	Antioxidant and antimicrobial properties	
Epoxylnostan	Reduce oxidative damage and support turgor pressure	
Hexatriacontane	Antioxidant property	
Cyclopropaneoctanoic acid	Antioxidant and antimicrobial properties	
Succinic acid	Plant growth promotion	
Benzothiazole	Antimicrobial property	

Surface Topography (CASTp) was utilized to identify the active binding locations of the protein (<http://sts.bioe.uic.edu/castp/index.html>).¹⁵¹ For ligand production, the metabolites from root exudates were chosen, and their structures were obtained from PubChem in a structured data file.¹⁵² The AutoDock Vina module in PyRx 0.8 and BIOVIA Discovery Studio Visualizer (<https://www.3ds.com/products-services/biovia/>) were employed for molecular docking to evaluate binding energies and ligand-receptor interactions.¹⁵³

Among the identified compounds evaluated against the salinity and drought-responsive protein (Figure 8(C) and (D)), Epoxylnostan interacts with the DREB (dehydration-responsive element-binding) protein with a binding affinity of -7.1 kcal/mol, forming hydrogen bonds with TRP 63. As DREB proteins regulate stress-responsive gene expression, this interaction suggests a possible role of Epoxylnostan in stress mitigation. Similarly, syntaxin-binding protein, which is involved in vesicular trafficking and cellular stress adaptation, binds Epoxylnostan with a higher affinity of -7.4 kcal/mol, forming hydrogen bonds with ASN 173 and engaging in Van der Waals interactions with THR 87, GLN 163, ILE 175, and VAL 174. Conversely, acetic acid displayed the lowest binding affinity, with



Under drought stress, VIT1 Channel Protein (Vacuolar Iron Transporter 1), crucial for ion homeostasis, interacts with Quassin (−6.1 kcal/mol), forming hydrogen bonds with TYR 254 and GLN 250, suggesting a role in maintaining ionic balance under saline conditions. LEA (Late Embryogenesis Abundant) protein, which plays a protective role against dehydration-induced damage, binds strongly with Quassin (−8.4 kcal/mol). The interaction involves hydrogen bonding with ASN 173 and Van der Waals interactions with ILE 175, GLY 105, GLY 85, and THR 87. This suggests that quassin may help stabilize cellular proteins and maintain structural integrity under water-deficient conditions. Conversely, the ligand acetic acid displays the lowest binding affinities of −2.8 kcal/mol in VIT 1 channel protein and −3.1 kcal/mol in LEA 3 protein (Table 4). The inoculation of *Bacillus pseudomycoides* augmented the

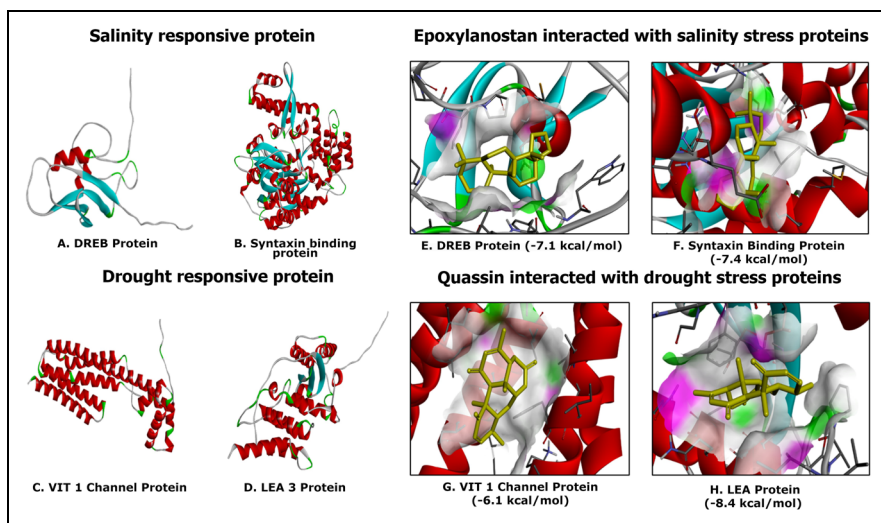


Figure 8. Molecular docking analysis of stress-responsive proteins. Images A and B represent salinity-responsive proteins, where A (DREB protein) and B (syntaxin-binding protein) are involved in salinity stress response. Docking analysis shows that Epoxylnanostan interacted with E (DREB protein) at -7.1 kcal/mol and F (syntaxin-binding protein) at -7.4 kcal/mol. Similarly, Images C and D correspond to drought-responsive proteins, specifically C (VIT1 channel protein) and D (LEA3 protein). Docking results indicate that Quassin interacted with G (VIT1 channel protein) at -6.1 kcal/mol and H (LEA protein) at -8.4 kcal/mol.^{147–150}

expression of the *Dreb1* gene using volatile chemicals. Molecular docking revealed two compounds, 2,6-ditert-butylcyclohexa-2,5-diene-1,4-dione, and 3,5-ditert-butylphenol, with binding energies of -6.2 and -6.5 kcal/mol, respectively, suggesting their potential to inhibit MYB (myeloblastosis protein) protein production under drought stress conditions.¹⁵⁴ Similarly, essential oils, particularly taxol, augment drought resilience in *Eucalyptus grandis* by influencing the VIT1 protein. Molecular docking and dynamics simulations demonstrate that the Taxol-6IU4 complex exhibits considerable binding affinity and stability, implying that this interaction may enhance drought resistance in plants.¹⁴⁹ The incorporation of quercetin dihydrate into the active region of syntaxin proteins may impair their functionality, therefore affecting downstream processes in Chinese flowering cabbage to mitigate salinity stress effects.¹⁵⁵ Nonetheless, the molecular mechanisms underlying drought tolerance in mung beans, emphasizing molecular docking and molecular dynamics simulations to investigate interactions between ABA agonists and a modelled drought-related protein, reveal prospective avenues for improving drought resilience. Epoxylnanostan and quassin, exhibiting significant binding affinity for drought and salinity proteins, indicate potential functions in stress tolerance, establishing them as attractive candidates for further research on abiotic stress.

Table 4. Binding energies and interacting residues of root exudate metabolites with salinity and drought-responsive protein.

Condition	Target protein	Compound name	Binding affinity (kcal/mol)	Residues involved in Hydrogen bond formation	Residues involved in Vander Waals attraction
Salinity stress	DREB protein Syntaxin-binding protein	Epoxylnostan	−7.1	TRP 63	CYS 94
		Epoxylnostan	−7.4	ASN 173	THR 87, GLN 163, ILE 175, VAL 174, THR 87
Drought stress	VIT I channel protein	Quassin	−6.1	TYR 254, GLN 250	TYR 140, GLU 141
	LEA protein	Quassin	−8.4	ASN 173	ILE 175, GLY 105, GLY 85, THR 87

Limitations of microbial inoculants in groundnut cultivation

Though microbial inoculants benefit groundnut production in numerous aspects, they temporarily alter the indigenous beneficial soil microbial communities resulting in a shift in microbial diversity and function. Direct effects include competitive, inhibitory (antagonism), or synergistic microbial interaction while the indirect effects include modifications in root exudate patterns and metabolites influencing soil microbial communities.¹⁵⁶ It may disrupt the essential biological processes occurring in soil such as nutrient cycling, organic matter decomposition, plant-microbe interaction, natural symbiosis, biocontrol, and biodegradation of contaminants. Therefore, it is necessary to ensure the safety of indigenous species. A better understanding of strains, their adaptability, interaction studies with other microbes, and field evaluation and site-specific testing of microbe-based inoculants under varied soil types and environmental conditions are needed to ensure the consistent performance of microbial inoculants.¹⁵⁷ Assessment of soil microbiome to select compatible microbial strains with native microbiota, adopting co-inoculation or consortia or synthetic microbial communities (SynCom) promote synergistic benefit, employing molecular methods including metagenomics and qPCR helps in monitoring inoculation impacts on soil microbiota, addition of organic amendments and sustainable agricultural practices could potentially improve the benefits of microbial inoculants. SCAR (sequence characterized amplified region) markers specifically identify the introduced strains from the native microbiota. Knocking out of specific genes from the microorganism could be effectively used to study their role in plant-microbe interaction. Developing new formulation techniques such as polymer-based encapsulation and freeze-dried powder to enhance the shelf life and stability of microbial inoculants. Ensuring regulatory framework prevents the contamination of the environment.

Conclusion

Microbial inoculants play a key role in sustainable groundnut production by enhancing plant growth, facilitating nutrient uptake, improving soil fertility and microbial diversity, augmenting the plant's resilience to environmental stresses, and reducing the dependence on chemical inputs. This review highlighted the significance of groundnut-associated microorganisms, their mechanisms of plant growth promotion, their functional role in drought and salinity stress alleviation, and their effects on root exudate metabolites in stress signalling. Molecular docking studies further revealed the interactions between these metabolites and key stress-responsive proteins (DREB, Syntaxin, VIT1, LEA), demonstrating their role in plant stress adaptation. This review emphasizes the need to integrate microbial inoculants with organic amendments for long-term soil fertility and productivity. Policy support, research investments, and large-scale field trials are crucial for the widespread adoption and practical implementation of bioinoculants in sustainable groundnut cultivation.

Future thrust

The isolation and characterization of native microbial strains are crucial for enhancing sustainable groundnut production. The application of culture-independent methods to investigate soil microbial communities and reveal the functional and taxonomic diversity of indigenous microorganisms in response to bio-inoculant introduction remains to be clarified. The inquiry is necessary to determine the precise mechanisms by which the inoculant confers benefits. Many beneficial microbes are utilized as inoculants and are anticipated to possess multiple modes of action, which can be leveraged in various manners contingent upon the conditions at the inoculation site.


To optimize the use of microbial inoculants, a more systematic approach is required in strain selection, considering environmental parameters, microbial persistence, and interactions within microbial communities. Researchers should mainly focus on strain selection, its mechanisms, and multisite trials to assess their efficacy across diverse agro-climatic conditions, extending the technology from lab to land. Synthetic microbial communities offer a promising strategy to study and harness complex microbial interactions for improved plant resilience and productivity. Moving beyond single-strain inoculants, formulating SynCom-based inoculants can enhance microbial cooperation, nutrient acquisition, and stress adaptation in groundnut cultivation.

The adoption, integration, and optimization of microbial inoculants, along with organic amendments ensure long-term soil fertility, lower input costs, and benefit farmers through higher yield. Through provision subsidies, the establishment of regulatory frameworks for quality control, allocation of funds for research grants, and extension services to enhance farmers' awareness could promote sustainable soil health. By integrating microbial inoculants with modern biotechnological approaches, we can advance groundnut production systems toward enhanced yield, resilience, and environmental sustainability.

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ORCID iDs

Kaviya Sree Krishnan  <https://orcid.org/0009-0003-5856-1804>

Anandham Rangasamy  <https://orcid.org/0000-0002-3496-564X>

Yuvasri Errakutty Arunan  <https://orcid.org/0009-0009-0693-7084>

Authors contribution

KKS contributed to writing the original draft, visualization, formal analysis, data curation, and conceptualization. RA contributed to reviewing and editing, supervision, resources, formal analysis, data curation, conceptualization, and validation. EAY contributed to writing, formal analysis, data curation, and conceptualization. DB, ST, and SV contributed to the formal analysis and review of the manuscript.

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Data availability statement

The data supporting the findings of this study are available from the corresponding author upon reasonable request.

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