



Review

Unveiling the roles, mechanisms and prospects of soil microbial communities in sustainable agriculture

Kelvin Kiprotich^{1,3}  · Esther Muema¹ · Clabe Wekesa² · Tavasi Ndombi³ · John Muoma³ · Dennis Omayio³ · Dennis Ochieno³ · Hamond Motsi¹ · Siphon Mncedi¹ · Janet Tarus³

Received: 22 October 2024 / Accepted: 3 February 2025

Published online: 17 February 2025

© The Author(s) 2025 

Abstract

Soil hosts diverse microbial communities including bacteria, fungi, archaea, protozoans and nematodes among others, which are fundamental to sustainable agriculture and drive essential processes that underpin soil fertility, plant health, and ecosystem resilience. They promote plant growth through mechanisms like nitrogen fixation, phosphorus solubilization, production of growth-promoting substances, enhancement of nutrient uptake, improvement of soil structure and detoxification of harmful substances. Recently, there has been increasing interest in utilizing microorganisms to improve soil health and boost plant growth and efficiency, despite limited understanding of microbial diversity, microbe-plant interactions, and translating laboratory findings to field conditions. This interest is driven by the urgent need to feed the growing global population, placing pressure on arable land to produce high-quality yields. Conventionally, synthetic fertilizers have been extensively used to provide nutrients, promote plant growth, and increase crop productivity. Although synthetic fertilizers have revolutionized agriculture since the green revolution, their overuse has significantly harmed soil health, and reduced crop productivity. This review synthesizes the current knowledge on the mechanisms by which soil microbes influence sustainable agricultural practices, with a focus on soil nutrient cycling and plant-microbe interactions. We discuss the functions and mechanisms of important microbial groups, such as nitrogen-fixing bacteria, phosphorus-solubilizing bacteria (PSB), and fungi. Furthermore, we discuss the factors that influence soil microbial communities and highlight gaps in future research to maximize their potential use in agriculture. Understanding the significance and key mechanisms of microbial communities increases the potential of harnessing soil microbes as vital contributors to soil health and sustainable agriculture.

Keywords Nitrogen fixation · Phosphorus solubilizing bacteria · Soil microorganism · Soil health

1 Introduction

Soil serves as a habitat for a wide variety of microorganisms that play crucial roles in soil health, ecosystem stability, plant growth promotion, and productivity. These microbes encompass a diverse array of bacteria, fungi, actinomycetes, nematodes, protozoans, algae, protozoans and other soil micro faunal invertebrates that form symbiotic or associative relationships with plants, providing various benefits. Soil bacteria are the most abundant microorganisms

✉ Kelvin Kiprotich, kiprotichkelvin29@gmail.com; ✉ Esther Muema, emuema@sun.ac.za | ¹Department of Soil Science, Faculty of Agrisciences, Stellenbosch University, Private Bag X1, Matieland, Stellenbosch 7602, South Africa. ²Max Planck Institute for Chemical Ecology, Beutenberg Campus, Hans-Knöll-Str. 8, 07745 Jena, Germany. ³Department of Biological Sciences, School of Natural Sciences, Masinde Muliro University of Science and Technology, P. O. Box 190, Kakamega 50100, Kenya.



in soil and their numbers range from 10^8 to 10^9 billion cells per gram of soil followed by fungi and actinomycetes respectively [1–4] (Table 1). Each group of these soil microorganisms interacts with plants in unique ways, offering specific benefits for plant growth and development. For example, free-living nitrogen-fixing organisms such as *Azotobacter*, *Clostridium*, and *Cyanobacteria* naturally inhabit the soil, where they convert atmospheric nitrogen (N_2) into ammonia (NH_3). This NH_3 is then converted into ammonium (NH_4^+) and nitrate (NO_3^-), forms that plants can absorb. In contrast, symbiotic diazotrophs, such as *Rhizobium* and *Bradyrhizobium* form symbiotic relationship with host plants, like legumes, and provide fixed nitrogen in exchange for carbon compounds to fulfil their energy needs [5, 6]. Others inhabit plant rhizosphere which include PSB microbes that intermediate in transforming insoluble phosphorus complexes into forms accessible to plants [7, 8].

Additionally, mycorrhizal fungi form symbiotic associations with plant roots, enhancing nutrient uptake, particularly phosphorus, in return for carbohydrates [9] and controlling plant diseases [10]. Ferris [11] also described soil nematodes as playing a vital role in maintaining the structure and function of the soil food web. These nematodes precisely control the population of other soil organisms, contribute to soil aggregation and aeration, supply food for other soil organisms, and consume organisms that spread plant diseases. Generally, by living in the rhizosphere of plant roots, forming symbiotic relationships or living freely in the soil, microorganisms contribute to soil fertility and promote the growth of nutrient-demanding crops.

Some soil microorganisms also act as biocontrol agents against plant pathogens. Certain bacteria and fungi produce antimicrobial compounds or compete with pathogens for resources, thus suppressing harmful organisms and reducing plant disease incidence. Moreover, some have been genetically engineered to produce enzymes and hormones, using various plant extracts and microorganisms such as bacteria, fungi, viruses, and microalgae to develop strong antimicrobial activities against plant pathogens [15]. For example, some bacteria have been discovered to produce peptides, cyclic lipopeptides, and polyketides, which primarily target fungal pathogens [16, 17]. Furthermore, soil microbes assist plants in tolerating various environmental stresses, such as drought, salinity, and extreme temperatures. They achieve this by producing stress-related hormones, enzymes and exudates, which trigger plant root mechanisms to efficiently enhance water and nutrient uptake, thereby improving plant tolerance against salinity conditions. Besides salinity, plant microbe association suggest that there are unknown molecular mechanisms reshaping the rhizosphere biota and the plant physiology to cope and adapt to drought stress and extreme temperatures [18].

Consequently, utilizing soil microorganism that promote plant growth and improve soil health aligns with principles of the United Nations Sustainable Development Goal of Zero Hunger and specifically targets sub-goal for sustainable food production using resilient agricultural practices, particularly by reducing the reliance on anthropogenic activities that degrade soil [19]. By enhancing soil fertility, nutrient cycling, and improving plant health and growth, soil microorganisms contribute to agro-ecological practices that promote long-term productivity and environmental conservation [20]. They provide a comprehensive view of soil ecosystems beyond just physical and chemical properties, helping to ensure the long-term productivity and environmental sustainability of soils.

In essence, plant-promoting microbes represent a promising avenue for revolutionizing agriculture, offering major benefits to conservation, regenerative and sustainable agriculture. An indulgent approach to interactions between plants and soil microbes opens up exciting opportunities to enhance agricultural systems and address global challenges in food security, climate sustainability, and biodiversity and ecosystem sustainability [21]. The aim of this review was to explore the roles of soil microorganisms in sustainable agriculture, with a keen interest in key microbial groups, including

Table 1 Typical summary range of numbers and biomass for different microbial groups found in the top 0–6 inches (0–15 cm) of soil

Microbial Group	Relative Number (cells/g of soil)	Biomass ($\mu\text{g/g}$ of soil)	References
Bacteria	10^8 – 10^9	40–500	[1–4]
Fungi	10^4 – 10^6	100–1500	[1, 12]
Actinomycetes	10^6 – 10^8	10–100	[1]
Protozoa	10^3 – 10^5	1–10	[1]
Algae and Cyanobacteria	10^3 – 10^5	1–10	[1]
Archaea	10^6 – 10^7	10–50	[1–3]
Nematodes	10^2 – 10^3	1–100	[1, 13, 14]

Varies widely depending on several factors such as soil type, climate, vegetation, and land use

nitrogen-fixing bacteria, PSB, and fungi. It also examined the factors affecting soil microbial communities and pointed out areas for future research to enhance their application in agriculture.

2 Roles of soil microbial communities in sustainable agriculture

In recent years, there has been growing interest in harnessing the power of soil microorganisms in sustainable agriculture due to their essential roles in biogeochemical processes and other functions and services, such as soil structure formation, bioremediation, and the maintenance of plant health (Fig. 1) [22, 23]. These processes ensure the efficient recycling of essential nutrients, such as nitrogen, phosphorus, and carbon, maintaining soil fertility and supporting plant growth and development. Soil microbial communities act as ecosystem engineers by influencing soil aggregation, water retention, aeration, and root growth, creating a more robust and productive agricultural environment. Recent studies emphasize the synergistic interactions within diverse microbial communities, which support soil health and stimulate plant growth through intricate relationships, such as mutualistic symbiosis [20, 22, 24]. Furthermore, their diversity in soil enhances resilience to stress, facilitates adaptation to changing conditions, and ensures the continuity of vital ecosystem functions like nutrient cycling and carbon sequestration. For example, fungi are linked with the glomalin protein which is responsible for soil carbon storage and aggregate stability [25]. Therefore, preserving microbial diversity through practices like crop rotation, organic farming, and minimizing pesticide use can improve soil structure, boost nutrient availability, and support long-term soil fertility [26–28].

Soil microbes also play as biological control of soil-borne diseases through competitive exclusion and antibiosis mechanisms [29]. Advances in microbiome research have identified specific microbes that can suppress plant diseases like *Fusarium*, *Rhizoctonia*, and *Phytophthora*, which could revolutionize integrated pest management strategies in agriculture [16, 30]. Soil microbes have been isolated and applied in synthetic biology and new insights offer the potential to engineer microorganisms through advanced molecular techniques for specific agricultural or environmental functions,

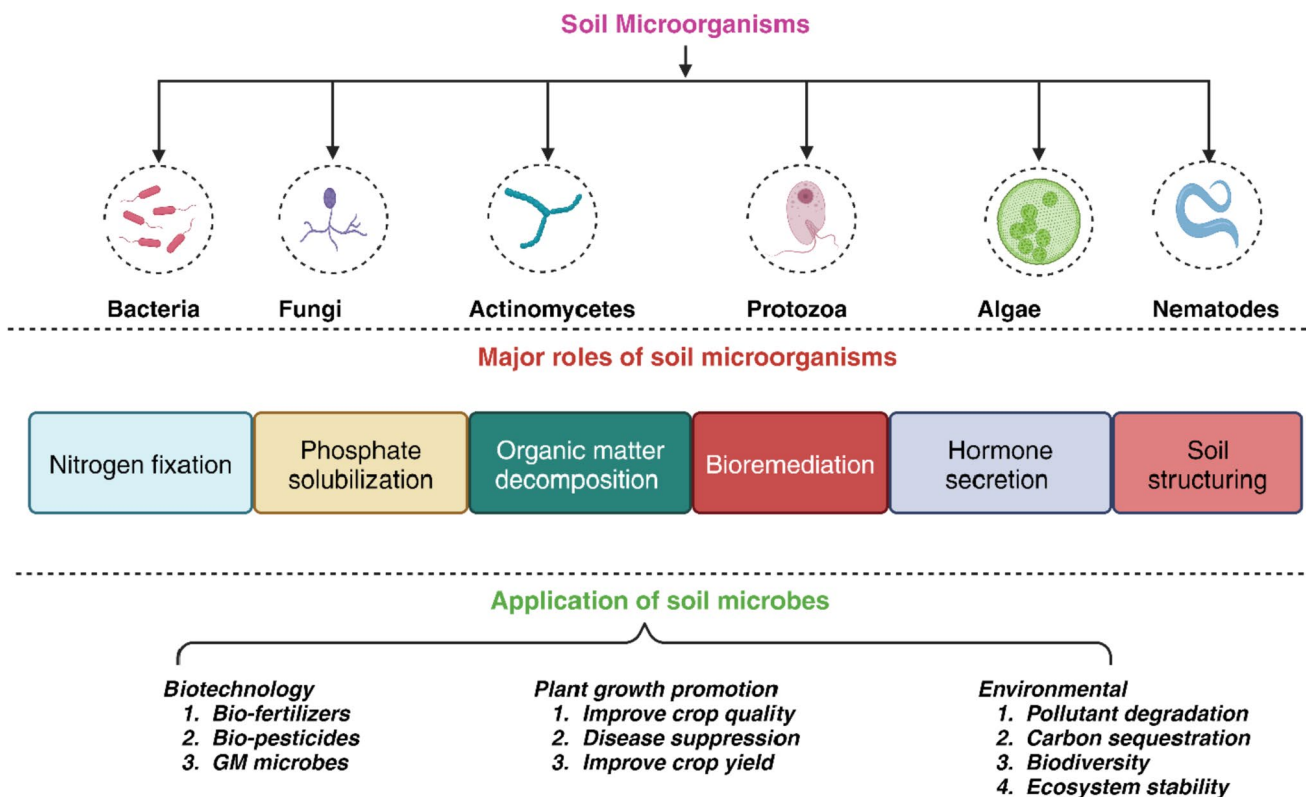


Fig. 1 Schematic illustration of soil microbes, their roles and applications in biotechnology, agriculture and environment. Source, this review. BioRender.com/v08n637

such as enhanced nutrient fixation, pollution degradation, resistance to pathogens, biofertilizers, biopesticides and carbon sequestration (Fig. 1).

These roles have significantly redesigned our insights into how life in soils function and how they can be managed for long-term agricultural productivity and soil health. Soil health management is changing because of the identification of soil microbial populations as crucial components and utilizing them in farming systems that are more robust, productive, and ecologically friendly by promoting microbial diversity, improving microbial functions, and incorporating microbial-based solutions into agricultural methods [31]. These innovative viewpoints offer fresh approaches to attain environmental sustainability, food security, and climate change mitigation in addition to challenging conventional agricultural methods. Agricultural practices that prioritize soil microbial health, including reduced tillage, crop rotation, organic farming, and agroforestry, are gaining recognition as essential components of sustainable agriculture [27, 28, 31]. These approaches foster the proliferation of beneficial microbes, support microbial biodiversity, and contribute to improved soil fertility, enhanced disease resistance, and healthy ecosystem services.

3 Soil bacteria

Soil bacteria are involved in various processes that are essential for plant growth and ecosystem stability. They inhabit the soil and then colonize plant rhizosphere (rhizosphere bacteria or rhizobacteria), reside in plant root tissues (endophytic bacteria), or on the plant root surface (epiphytic bacteria) [32]. Quantitative assessments of soil bacterial populations serve as critical indicators for evaluating soil health, enabling the determination of microbial diversity and abundance, which subsequently reflects the significance of bacterial activities in soil ecosystems. Such understanding helps in grasping ecosystem dynamics, monitoring environmental impacts, and guidance on sustainable land management practices. Listed in the subsequent subsections are some key plant growth-promoting bacteria (PGPB) that enhance plant growth and health through various mechanisms.

3.1 Nitrogen fixing bacteria

Nitrogen is one of the essential macronutrients required for plant growth and development, while it is also the most limiting. It is a crucial component of amino acids which are the building blocks of proteins. Proteins are essential for various biological processes in plants, including cell structure, enzyme functions, and metabolic pathways. Therefore, nitrogen is indispensable for the synthesis of proteins necessary for plant growth, development, and overall health. It is also vital in chlorophyll formation, making it essential for photosynthetic activity. Other functions of nitrogen include the promotion of vegetative growth, enhancing yield and quality, and finally, the regulation of metabolic processes [33].

In soil, nitrogen is present predominantly in two main forms: inorganic form making up to about 2%, while organic forms account for approximately 98% [24]. The inorganic forms comprise of NH_3 , NH_4^+ , NO_2^- , and nitrites (NO_3^-). Organic nitrogen is found in living or non-living organic matter such as soil biota, live animals and plant remains. Biological nitrogen is not directly available to plants and must be converted through the mineralization process to NH_3 or NO_3^- . This process is, however, very slow and its availability to plants is always competed by denitrification, soil erosion or leaching. To avail more N to plants, artificial inorganic nitrogen fertilizers using fossil fuels have been introduced to compensate for N deficiency in the soil [34]. Synthetic N is, however, detrimental to soil because it leads to pollution which adversely affects soil health and environment at large. To reduce this problem, the use of nitrogen-fixing bacteria as an alternative is considered an environmentally friendly solution.

Nitrogen-fixing bacteria collectively referred to as diazotrophic communities are microorganisms that are responsible for converting atmospheric nitrogen into forms that plants can use through a process called biological nitrogen fixation (BNF) [35]. They either form symbiotic relationships with host leguminous plants such as common beans (*Phaseolus* spp.), soybeans (*Glycine max*), peas (*Pisum* spp.), lentils (*Lens culinaris*), chickpeas (*Cicer arietinum*), peanuts (*Arachis hypogaea*), clover (*Trifolium* spp.), lupins (*Lupinus* spp.) and alfalfa (*Medicago sativa*) among others, or live freely in soils. Nodulating bacteria collectively known as rhizobia infect the host plant roots or stems, forming specialized structures known as nodules, where they multiply, and at maturity convert atmospheric nitrogen into ammonia, providing a crucial nitrogen source for the plant. These bacteria in return receive energy from the host plant in the form of photosynthates. Similarly, the non-nodulating free-living soil bacteria also contribute to soil fertility by converting atmospheric nitrogen into inorganic forms usable by plants [36]. Examples of bacteria well known for biological nitrogen fixation through nodulation include members of *Rhizobium* [37], *Bradyrhizobium* [38], *Frankia* [39], *Mesorhizobium* [40], *Sinorhizobium/Ensifer*

[41], *Paraburkholderia* [42], *Microvirga* [43] and *Methylobacterium* [44] among others. Members of free living nitrogen-fixing bacteria include *Cyanobacteria* (blue-green bacteria), *Clostridium*, *Azotobacter*, *Burkholderia*, *Klebsiella*, *Derxia* and *Azorhizobium* among others [45–48] (Table 2).

3.1.1 Mechanism of biological nitrogen fixation

The principal mechanism of biological nitrogen fixation involves the enzyme nitrogenase, which catalyzes the reduction of atmospheric N_2 to NH_3 . The process begins when nitrogen fixing bacteria cells in the soil recognize specific chemical signals, collectively known as flavonoids released by plant roots in response to nitrogen deficiency in soil. In response to these signals, the bacteria *nodD* gene triggers transcription of *nod* genes (*nodA*, *nodB*, *nodC*, *nodE*, *NodL* and *nodM*) and encode enzymes (e.g. *Acytransferase*, *chitin deacetylase* and *chitin synthase*) and proteins (e.g. *Symbiotic Receptor-like Kinase*, *Symbiosis-Specific Remorin*, *Nuclear Factor Y*, *Subunit A1* and *Calcium-Dependent Protein Kinases*,) that facilitate the production of nodulating factors which are recognized by plant receptors. Most bacteria infect the root hairs and then initiate root curling and nodule formation [99, 100]. Once inside the root nodules, the bacteria differentiate into bacteroids, specialized forms capable of nitrogen fixation, and provide fixed nitrogen to the host plant (Fig. 2). They do so by undergoing morphological and physiological changes, including cell elongation and increased cell membrane permeability and utilization of plant carboxylates [101]. In the absence of oxygen during this symbiotic association, the nitrogenase enzyme complex system consists of two main components: iron (Fe) and molybdenum-iron (MoFe) proteins. The Fe protein acts as a shuttle, transferring electrons from a donor to the MoFe protein, where nitrogen fixation occurs.

The MoFe protein contains the active site where nitrogen reduction takes place, requiring a constant supply of energy in the form of ATP [35]. The electrons necessary for nitrogen reduction are provided by electron donors such as reduced ferredoxin or flavodoxin. Nitrogenase is highly sensitive to oxygen and is irreversibly inhibited by its presence. Therefore, nitrogen-fixing bacteria creates anaerobic conditions within specialized cellular structures to protect nitrogenase activity. In the case of symbiotic nitrogen-fixing bacteria such as *Rhizobium*, specialized root nodules are formed on the host plant's roots, providing an environment conducive to nitrogen fixation. Free-living nitrogen-fixing bacteria may form cysts or spores or reside in oxygen-depleted soil microsites to avoid oxygen inhibition. Nitrogenase complex catalyzes the reduction of atmospheric N_2 and convert it to NH_3 in presence of energy in form of ATP. This ammonia is then utilized by both the plant and the bacteria for their nitrogen requirements [102] (Fig. 2).

3.1.2 Role of nitrogen fixing bacteria in sustainable agriculture

The ability of nitrogen-fixing bacteria to biologically fix atmospheric nitrogen allows leguminous plants to thrive in nitrogen-deficient soils and reduces the need for synthetic nitrogen fertilizers in agriculture. These bacteria establish a highly specific symbiotic relationship with leguminous plants. A diverse species of these microbes exhibit host specificity, meaning that different strains form symbiotic relationships with specific legume species while others are fix nitrogen without forming the relationship [24]. This specificity is determined by the compatibility between the bacterial nodulation genes and nodulation receptor proteins of the plant. *Rhizobium*-legume symbioses, for example, are highly co-evolved, with each partner exerting selective pressure on the other to maintain compatibility and optimize nitrogen fixation efficiency [103].

In agriculture, nitrogen fixing inoculants are commonly used to improve soil fertility and enhance crop yields in legume cultivation [40]. These inoculants consist of selected strains of rhizobia that are applied to seeds or soil prior to planting. By introducing compatible nitrogen fixing strains to the rhizosphere of leguminous crops, farmers can promote efficient nodulation and nitrogen fixation, leading to increased plant growth, productivity, and nitrogen inputs into the soil [23]. The use of rhizobia-based inoculants offers several environmental benefits. For example, by reducing the need for synthetic nitrogen fertilizers, inoculation with nitrogen fixing bacteria helps mitigate nitrogen pollution of water bodies or underground water, greenhouse gas emissions, and soil degradation associated with conventional agricultural practices [20]. Additionally, the nitrogen fixed by soil bacteria becomes available to subsequent crops or is retained in the soil, contributing to long-term soil fertility and sustainability. On-going research on elite inoculants of biological nitrogen-fixing bacteria focuses on understanding the molecular mechanisms underlying symbiotic interactions, enhancing the efficiency of nitrogen fixation, and expanding the range of legume hosts and other plants that can form symbioses with wide range of bacteria and fungi [104].

Similarly, those living without direct interaction with other organisms, for example, members of the genus *Azotobacter* are also being investigated. Genetic engineering techniques have also been explored to improve the performance of

Table 2 Various nitrogen-fixing bacteria, their mode of association, and origin

Species	Mode of association	Isolation source/host plant	Reference
<i>Anaeromyxobacter oryzae</i>	Free living	Paddy soil	[49, 50]
<i>Anaeromyxobacter soli</i> sp	Free living	Paddy Soil	[50]
<i>Anaeromyxobacter terrae</i> sp	Free living	Paddy Soil	[50, 51]
<i>Azospirillum lipoferum</i>	Free living	Soil	[52]
<i>Azotobacter beijerinckii</i>	Free living	Laboratory	[53]
<i>Azotobacter beijerinckii</i>	Free living	Wheat/Rice	[54, 55]
<i>Azotobacter chroococcum</i>	Free living	Cow dung compost	[56]
<i>Azotobacter vinelandii</i>	Free living	Soil	[57]
<i>Bacillus subtilis</i>	Free living	Cow dung compost	[56, 58]
<i>Bradyrhizobium diazoefficiens</i>	Symbiosis	Pigeon Pea	[59, 60]
<i>Bradyrhizobium japonicum</i>	Symbiosis	Soybean nodules	[61]
<i>Bradyrhizobium ottawaense</i>	Symbiosis	Soybean nodules	[62, 63]
<i>Bradyrhizobium shewense</i>	Symbiosis	<i>Erythrina brucei</i>	[64]
<i>Bradyrhizobium</i> sp.	Symbiosis	Serradella	[65]
<i>Bradyrhizobium symbiodeficiens</i>	Symbiosis	Hog Peanut	[66]
<i>Bradyrhizobium yuanmingense</i>	Symbiosis	Peanut	[38, 67]
<i>Bradyrhizobium</i> sp	Symbiosis	Coffee	[68]
<i>Burkholderia cepacia</i>	Symbiosis	Chickpea	[69, 70]
<i>Candidatus Phyllobacterium</i>	Symbiosis	Astragalus	[71]
<i>Ensifer medicae</i>	Symbiosis	Medic	[72, 73]
<i>Ensifer meliloti</i>	Symbiosis	Medic	[74]
<i>Klebsiella variicola</i>	Symbiosis	Sugarcane	[75]
<i>Kosakonia radicincitans</i>	Free living	Maize roots	[76]
<i>Mesorhizobium ciceri</i>	Symbiosis	Chickpea	[77, 78]
<i>Paenibacillus brassicae</i> sp	Free living	Cabbage	[79]
<i>Paenibacillus sinensis</i> sp	Free living	Wheat	[80]
<i>Paenibacillus vini</i> sp.	Free living	Fermentation pit	[81]
<i>Pseudomonas stutzeri</i>	Free living	Maize rhizosphere	[82]
<i>Raoultella electrica</i>	Free living	Midgut of insect	[83]
<i>Rhizobium anhuiense</i>	Symbiosis	Faba bean/Pea	[84]
<i>Rhizobium etli</i> and <i>R. Nodulate</i>	Symbiosis	Common bean	[85, 86]
<i>Rhizobium gallicum</i>	Symbiosis	Common bean	[87]
<i>Rhizobium mesosinicum</i>	Symbiosis	Coffee	[68]
<i>Rhizobium multihospitium</i>	Symbiosis	Coffee	[68]
<i>Rhizobium multihospitium</i>	Symbiosis	Chickpea	[88]
<i>Rhizobium pusense</i>	Symbiosis	Mung bean	[89, 90]
<i>Rhizobium leguminosarum</i>	Symbiosis	Clover	[91]
<i>Rhizobium sullae</i>	Symbiosis	Sulla	[92]
<i>Rhizobium tropici</i>	Symbiosis	Common bean	[93, 94]
<i>Rhizobium phaseoli</i>	Symbiosis	Common bean	[6]
<i>Sinorhizobium fredii</i>	Symbiosis	Wild Soybeans	[95]
<i>Sinorhizobium meliloti</i>	Symbiosis	Medic	[96, 97]
<i>Symbiovar Sojae</i>	Symbiosis	Soybean Nodules	[98]

beneficial strains under diverse environmental conditions and agricultural settings [105, 106]. Recent examples include modifications of *Agrobacterium rhizogenes* [107] and *Sinorhizobium meliloti* [108] using Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR) and CRISPR-associated protein 9 (CRISPR/Cas9) editing technology.

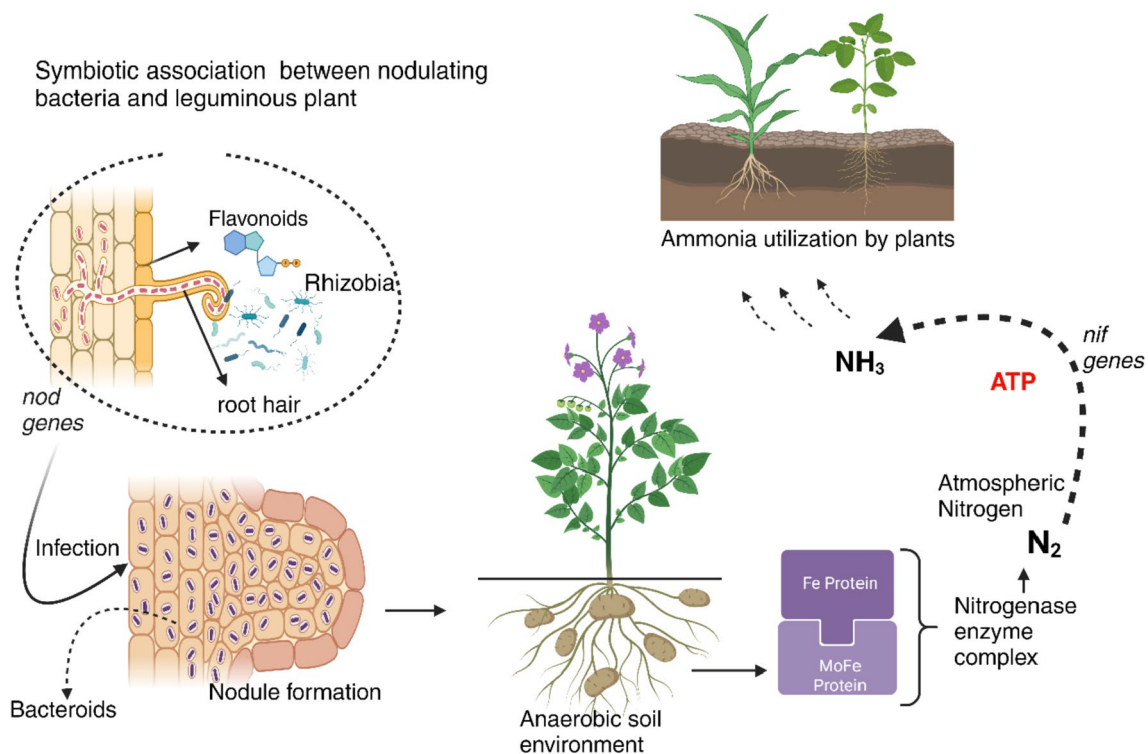


Fig. 2 The schematic illustration of the main steps involved in the nitrogen fixation process, including the recognition and infection of plant roots by nitrogen-fixing bacteria, the formation of nodules, the establishment of an anaerobic environment within nodules, the activation of nitrogenase enzyme complexes, and the conversion of atmospheric nitrogen into ammonia for plant utilization. Source, this review. BioRender.com/h22o238

3.2 Phosphorus solubilizing bacteria

P is a crucial macronutrient essential for plant growth and development, second only after N in importance. It plays a critical role during the early stages of plant growth. The main functions of phosphorus include energy storage and transfer, nucleic acid synthesis, formation and structuring of cell organelles, photosynthesis, cell division, shoot elongation, and root development [21]. When plants are deficient in phosphorus, they exhibit symptoms such as stunted growth, purplish leaves, weak stems, necrotic spots, leaf curling, poor flower and fruit development, delayed maturity, and ultimately reduced yields. In the soil, P exists in two forms: (i) organic P from decomposed plant and animal residues, which is not readily available to plants and requires mineralization, and (ii) inorganic phosphorus from mineral sources, often bound with other elements like aluminum (AlPO_4), iron (FePO_4), zinc ($\text{Zn}_3(\text{PO}_4)_2$), and calcium ($\text{Ca}_3(\text{PO}_4)_2$). These inorganic forms are available in very low quantities and are released slowly owing to their complex structure. Soil microorganisms help mitigate this issue by solubilizing phosphorus, thereby enhancing its availability for plant uptake and promoting growth and development.

PSB are highly effective microorganisms that make both organic and inorganic phosphorus compounds readily available for plant uptake [8]. These bacteria are found in diverse environments such as agricultural soils, the rhizosphere of plants, root nodules of leguminous plants, compost materials, water, sewage, and decaying organic matter. Examples of PSB that have been found to effectively solubilize and mineralize phosphorus include species from the genera *Agrobacterium* spp. [109], *Pseudomonas* spp. [110], *Bacillus* spp. [111], *Rhizobium* spp. [112], *Bradyrhizobium* spp. [113], *Enterobacter* spp. [7] and *Burkholderia* spp. [22]. Recent studies have also identified additional PSB such as *Azotobacter* spp. [55], *Kushneria* (90) spp. [114] *Paenibacillus* [115], *Rhodococcus* spp. [116], *Salmonella* spp. [117], *Sinomonas* spp. [118], *Thiobacillus* spp. [119], *Azospirillum* spp., *Klebsiella* spp., and *Serratia* spp. [8] (Table 3).

Table 3 Various bacterial species involved in phosphorous solubilization, and their origin

PSB	Source	Cultivated plant	References	
<i>Pseudomonas</i> spp.	Cultivated bulk soil	Wheat	[120]	
	Semiarid bulk soil	Wheat	[121, 122]	
	Rhizosphere soil	Poplar	[123]	
	Rhizosphere soil	Tomato	[124, 125]	
	Rhizosphere soil	Common bean	[7]	
	Cultivated bulk soil	Onion	[126]	
	Cultivated bulk soil	Groundnut	[127]	
	Rhizosphere soil	Wheat	[128]	
	Rhizosphere soil	Soybean	[129, 130]	
	Rhizosphere soil	Chilli	[131]	
<i>Enterobacter</i> spp.	Rhizosphere soil	Cabbage	[132]	
	Rhizosphere soil	Maize	[133]	
	Rhizosphere soil	Common bean	[7]	
	Rhizosphere soil	Wheat	[134, 135]	
	Cultivated bulk soil	Pepper	[136]	
	Rhizosphere soil	Rice and peanut	[137]	
	Rhizosphere soil	Sugarcane	[138]	
	Rhizosphere soil	Potatoes	[139]	
	Rhizosphere soil	Alfa alfa	[140]	
	Rhizosphere soil	Forage grasses	[141]	
	Rhizosphere soil	Grapevines	[142]	
	<i>Bacillus</i> spp.	Cultivated bulk soil	Rice	[143]
		Cultivated bulk soil	Wheat	[144]
Rhizosphere soil		Wheat, maize	[145]	
Rhizosphere soil		Wheat	[146]	
Rhizosphere soil		Tomato	[125, 147, 148]	
Cultivated bulk soil		Wheat	[120]	
Cultivated bulk soil		Groundnut	[149]	
Cultivated bulk soil		NT	[150]	
Rhizosphere soil		Guinoa	[151]	
Rhizosphere soil		Chickpea	[152]	
<i>Burkholderia</i> spp.	Rhizosphere soil	Pigeon pea	[153]	
	Cultivated bulk soil	NT	[154]	
	Cultivated bulk soil	Rice	[155]	
	Cultivated bulk soil	Corn, soybean, rice	[156]	
	Cultivated bulk soil	Tea	[157, 158]	
	Rhizosphere soil	NT	[159]	
	Soybean rhizosphere	Tomato	[160]	
	Rhizosphere soil	Barley	[161]	
	Rhizosphere soil	Rice	[162]	
	<i>Rhizobia</i> spp.	Root nodules	Soybean	[163]
Cultivated bulk soil		NT	[164]	
Root nodules		Soybean	[165]	
Root nodules		Several legumes	[166]	
Root nodules		Common bean	[6]	
<i>Azospirillum</i> spp.	Rhizosphere soil	Wheat	[167, 168]	
	Cultivated bulk soil	Maize	[169]	
<i>Serratia</i> spp.	Cultivated bulk soil	Onion	[126]	
	Cultivated bulk soil	Faba	[170]	
	Rhizosphere soil	Peanuts and Maize	[171]	
	Rhizosphere soil	Wheat	[172, 173]	
<i>Mesorhizobia</i> spp.	Rhizosphere soil and root nodules	Chickpea	[174, 175]	

NT- The strains were not tested with any plants but were evaluated in laboratory assays

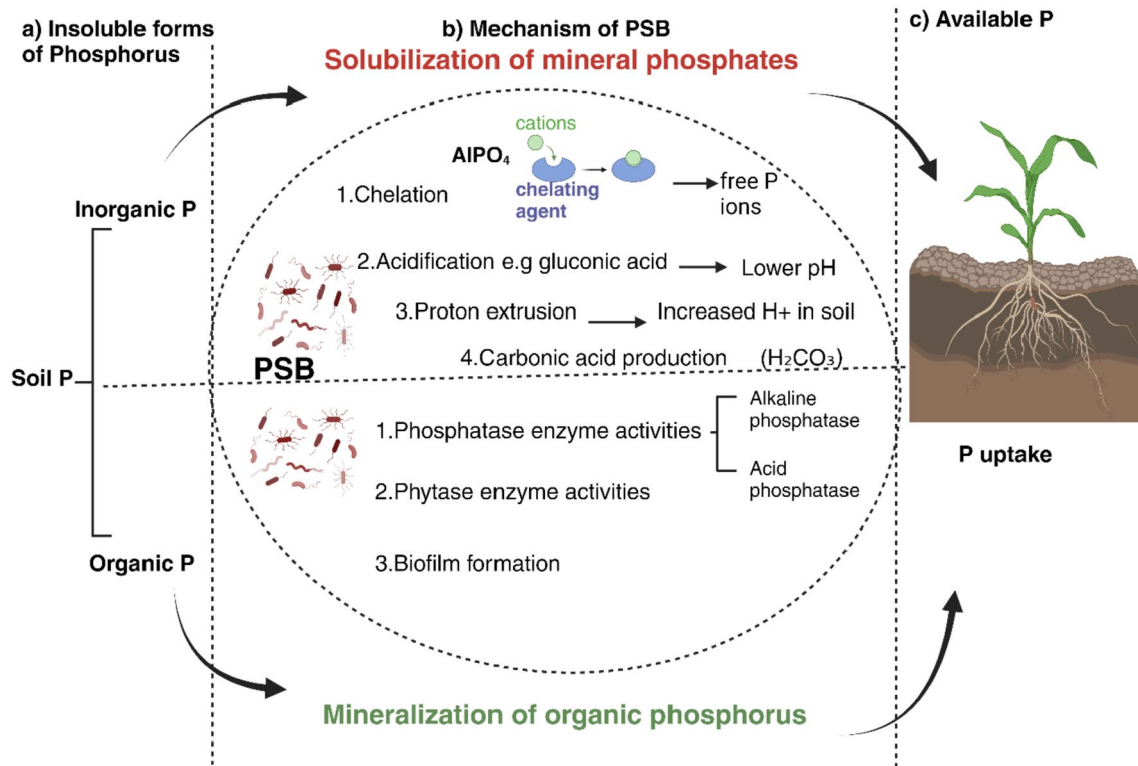


Fig. 3 A schematic illustration of the mechanisms of PSB through mineralization and solubilization of soil P into soluble forms for plant uptake. Source, this review. BioRender.com/p19q137

3.2.1 Mechanisms of phosphorus solubilizing bacteria

PSB utilizes two primary mechanisms: solubilization of mineral phosphates and mineralization of organic phosphorus. These mechanisms highlight the processes of inorganic phosphate solubilization and organic phosphorus mineralization together with other cascades of events in soil as described previously [109]. To solubilize mineral phosphates, bacteria produce organic acids, chelating agents, proton extrusion, and weak carbonic acid formation. For mineralization of organic and inorganic phosphorus, bacteria secrete phosphatase and phytase enzymes, modifying the soil environment and increasing phosphorus availability (Fig. 3).

In the acidification theory, hydrogen ions play a key role in the solubilization of mineral phosphate. PSB secretes various organic acids, such as citric acid, oxalic acid, lactic acid, gluconic acid, and acetic acid. These bacteria release acids through their oxidation and metabolic pathways into the periplasmic space, allowing organic acids to enter the soil environment and cause a pH decline [119]. The resulting decrease in pH leads to the release of free hydrogen ions (H^+) in exchange for cations present in the complexes, which then facilitates the dissolution of insoluble mineral phosphates, such as tricalcium phosphate and dicalcium phosphate, converting them into soluble phosphate ions ($H_2PO_4^-$, HPO_4^{2-}) available for plant uptake. Additionally, it has also been shown that the solubilization of mineral phosphate can occur in microbial cells and soil environment without production of organic acids through proton extrusion process. PSB participate actively in transportation of protons in form of H^+ ions from their cells into the surrounding soil environment, resulting in the solubilization of phosphorus without the production of organic acids [176]. Furthermore, the solubilization of mineral phosphates is achieved by PSB-producing chelating agents such as siderophores. Complexes, such as aluminum phosphate, zinc phosphate, and calcium phosphate, have strong metallic bonds, making phosphorus less available to plants. Chelating agents bind to metal ions (e.g., Ca^{2+} , Fe^{3+} , and Al^{3+}) that are commonly associated with these insoluble phosphate complexes, thus freeing the phosphorus for plant use [177].

To mineralize organic phosphorus, bacteria secrete enzymes such as phosphatases and phytases (Fig. 3). Alkaline phosphatase catalyzes the hydrolysis of phosphate substrates in alkaline soil environments, while acid phosphatase performs this function in acidic environments. Phytase specifically targets and hydrolyzes phytate (myo-inositol hexakisphosphate), a prevalent form of organic phosphorus in soil that is not directly available to plants. The secretion of phosphatase enzymes

is related to the combined but distinct functions of phosphomonoesterase (PME) and phosphodiesterase (PDE) [119]. PME catalyzes the hydrolysis of phosphate monoesters (acid and alkaline phosphatases) releasing inorganic phosphate and alcohol. PDE hydrolyzes diesters such as nucleic acids and phospholipids into phosphomonoesters (inositol phosphates and mononucleotides), which are then transformed into bioavailable inorganic phosphorus. PSB such as *Pseudomonas*, *Enterobacter*, and *Pantoea* enzymatically mineralize soil phosphorus into soluble forms using these processes [21, 119].

3.2.2 Utilizing PSB for agriculture

PSB typically improves soil fertility and supports sustainable agriculture by making natural phosphorus more accessible to plants, which reduces the necessity for chemical phosphorus fertilizers [71]. This not only decreases production costs for farmers but also reduces environmental pollution caused by the overuse of chemical fertilizers. To utilize PSB, it is necessary to isolate the bacteria from various environments and assess their efficiency both in the laboratory and in the field. The rhizosphere, which is known for its high microorganism density, is a preferred source for researchers seeking effective solubilizing bacteria. Nevertheless, other sources of PSB include soil, water, decomposing organic matter/plant residues, and root nodules (Fig. 4).

To identify effective PSB, bacteria are isolated and cultured using suitable culture media such as Pikovskaya, developed by Russian scientist Raisa Yakovlevna Pikovskaya in 1948 [178] and NBRIP (National Botanical Research Institute Phosphorus Growth Medium), considered as most efficient medium which was modified by Nautiyal in 1999 [179]. Pikovskaya medium comprises 10 g of glucose, 5 g of calcium phosphate ($\text{Ca}_3(\text{PO}_4)_2$), 0.5 g of ammonium sulfate ($(\text{NH}_4)_2\text{SO}_4$), 0.2 g of sodium chloride (NaCl), 0.1 g of magnesium sulfate (MgSO_4), 0.2 g of potassium chloride (KCl), traces of manganese sulfate (MnSO_4) and ferrous sulfate (FeSO_4) each at 0.002 g, 0.5 g of yeast extract and 15 g of agar.

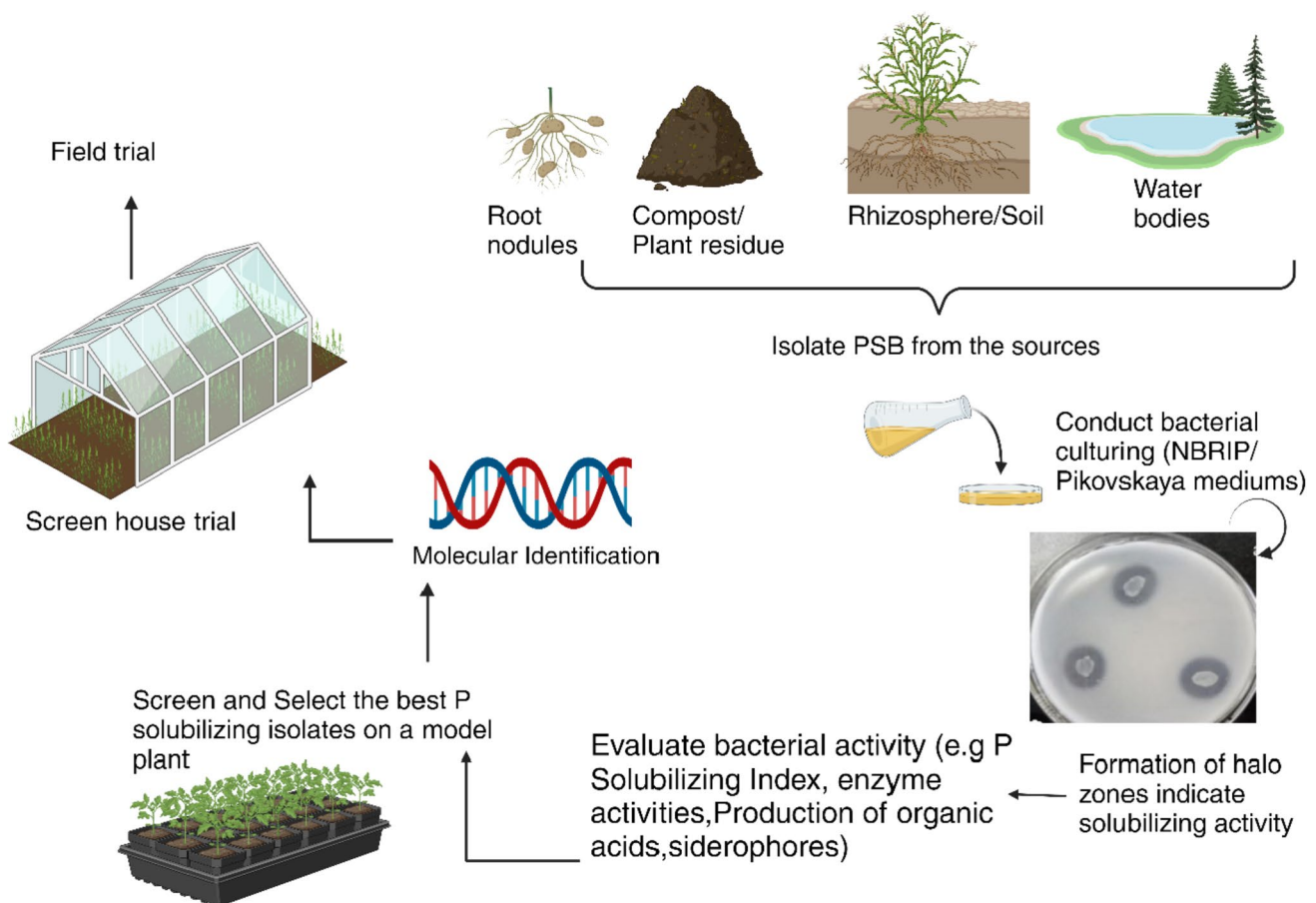


Fig. 4 Schematic representation of PSB isolation, culture, screening, molecular identification, and trials. Source, this review. BioRender.com/z52n260

NBRIP medium without yeast extract contains 10 g of glucose, 5 g of $\text{Ca}_3(\text{PO}_4)_2$, 0.5 g of $(\text{NH}_4)_2\text{SO}_4$, 0.2 g of NaCl, 0.1 g of $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.2 g of KCl, 0.002 g of $\text{MnSO}_4 \cdot \text{H}_2\text{O}$, 0.002 g of $\text{FeSO}_4 \cdot 7\text{H}_2\text{O}$ and 15 g of agar. After culturing, in-vitro visual assays are conducted to determine the solubilizing indices, as PSB grows and forms halo zones in the agar medium, differentiating efficient solubilizers from non-solubilizers. This is followed by a colorimetric analysis of released amount of phosphorus, phosphatase enzyme activities, phytase activity, among other measurements using broth medium. Once the efficient solubilizers are identified in the laboratory, the inoculants are prepared and screened under controlled conditions for plant growth promotion using a model plant in the screen house to further determine and select efficient isolates for use as biofertilizer (Fig. 4). To identify the isolated PSB at the species level, genomic distinctiveness, and phylogenetic relationships, several advanced molecular approaches have been used, including extracting the genomic DNA of the bacteria, amplification, sequencing using a reference database, and bioinformatics analysis to comprehensively study the genetic material for a deep understanding of molecular mechanisms [7, 119].

Extensive utilization of PSB in agriculture has been documented, and numerous strains have been identified as effective inoculants (Table 3). However, although experiments in controlled environments have been well-documented, field studies are comparatively limited, leading to an urgent need for further investigations. Implementing PSB inoculants has shown to enhance plant growth and development by increasing root and shoot biomass, improving root and shoot length, improving vegetative vigor and plant biomass and yield in various crops [120, 180–183]. These findings underscore the promising future of PSB in sustainable agriculture. It is then beneficial practice in soil amelioration which contributes significantly to microbial rhizosphere management and nutrient cycling for sustainable agriculture. More research in this area is necessary to unveil more beneficial PSB and test them under field conditions for agricultural sustainability and food production.

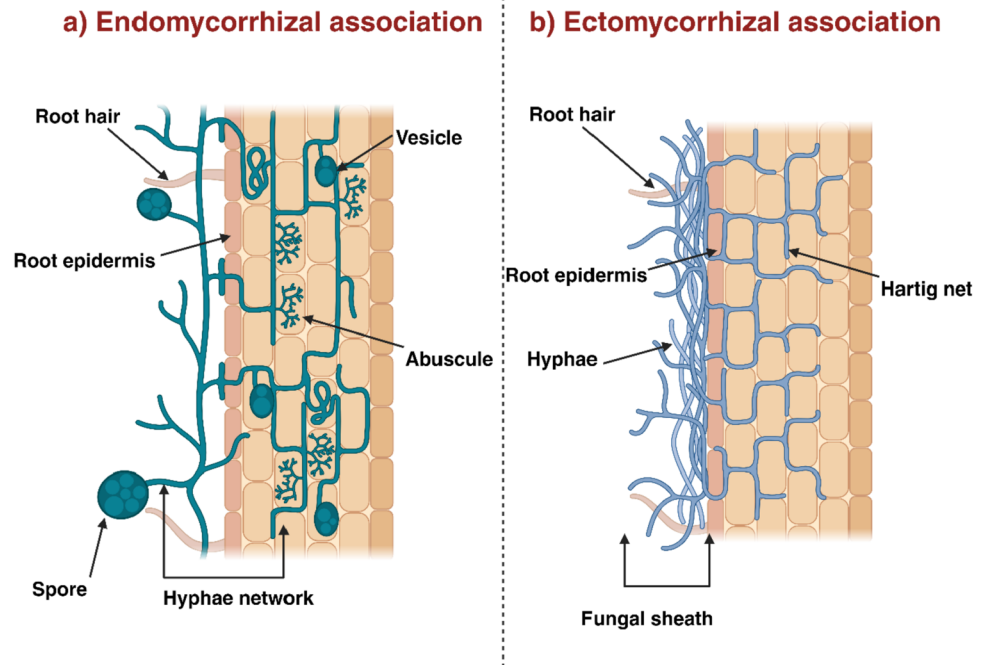
4 Soil fungi

Soil fungi are the second most critical microbes in the soil after bacteria, thriving even under adverse and unfavorable conditions due to their adaptability and high plasticity in response to physiological changes in the soil [184]. Fungi vary in size, ranging from microscopic spores that cannot be seen, to large fruiting bodies and other structures visible to the naked eye. Their primary function is to decompose organic matter and break down soil components, thereby balancing the ecosystem [185]. By secreting extracellular enzymes, fungi connect soil matter and plants, break down and decompose organic material, and play a vital role in nutrient cycling, particularly nitrogen and phosphorus. Although most fungi are beneficial, some fungi interact with other soil microorganisms, invade the plant materials and cause pathogenic effects leading to diseases.

Most beneficial fungi form symbiotic relationships with almost 90% of plants by forming hyphae networks. Fungi have filamentous bodies called hyphae that attach to the network of plant root hairs and acquire nitrogen, phosphorus, other micronutrients, and water in exchange for the carbohydrates produced by the plant. This mutually beneficial symbiotic relationship is termed as mycorrhizae network. Examples of fungi that participate in this symbiotic relationship include arbuscular mycorrhizal fungi (AMF) and ectomycorrhizal fungi [17, 186]. AMF are considered the most beneficial group of endophytic fungi, providing comprehensive benefits to plants, including tolerance to various stressful situations such as heat, salinity, drought, metals, and extreme temperatures [185]. AMF has been categorized taxonomically, primarily under the phylum *Glomeromycota*. They are classified into the orders *Glomerales*, *Archaeosporales*, *Paraglomerales*, and *Diversisporales*. The prominent families within these orders are *Glomeraceae*, *Gigasporaceae*, and *Acaulosporaceae*. The genera included in these families are *Glomus*, *Sclerocystis*, *Acaulospora*, *Entrophospora*, *Gigaspora*, and *Scutellospora* [187].

Members of the ectophytic fungi belonging to the phylum *Ascomycota* have long been known to be efficient antagonists of plant pathogenic microorganisms. Some recently investigated and confirmed to be beneficial include genera *Trichoderma* spp. *Aspergillus* spp. *Amanita* spp. *Boletus* spp. and *Laccaria* spp. and *Penicillium* spp. [188, 189]. Conversely, fungi from the Phylum *Basidiomycota* are primarily recognized for their role as decomposers. They secrete extracellular enzymes that enable the breakdown of lignin and the decomposition of organic materials like dead plants and wood, thus recycling nutrients back into the soil. This capability makes them important in bioremediation because they can degrade various pollutants, including pesticides and heavy metals in soil and water environments. Research has utilized these fungi to clean up contaminated soils and enhance the health of agricultural land [186, 190]. Some important species of this phylum that have proven agricultural benefits include; *Agaricus bisporus* [191], *Lentinula edodes* [192], *Pleurotus ostreatus* [193], *Tricholoma matsutake* [194], *Ganoderma lucidum* [195], *Phanerochaete chrysosporium* [196], *Coprinus comatus*, *Armillaria mellea* and *Scleroderma citrinum* [197].

Fig. 5 Schematic illustration of mycorrhizal association of soil fungi. **a** Endomycorrhizae association (arbuscular mycorrhizal fungi) and **b** ectomycorrhizal association. Source, this review. BioRender.com/o59n550



4.1 Mechanisms via which soil fungi support plants

Soil fungi primarily function by forming mycorrhizal associations with plants, which can be categorized into two types: Ectomycorrhizal and Endomycorrhizae (Arbuscular Mycorrhizal) associations [185]. Ectomycorrhizal association is where fungi envelop the surface of the plant's epidermal roots, forming fungal sheath without forming arbuscules. Instead, they form a Hartig network and extend hyphae into the soil to boost nutrient absorption, particularly phosphorus and nitrogen, and other nutrients required by the plants. Endomycorrhizae on the other hand, is where fungi penetrate plant root cells, forming complex structures known as arbuscules and vesicles inside the dermal cells of plant tissues (Fig. 5).

Endomycorrhizal association is commonly found in herbaceous plants and food crops. Both associations are mutualistic, benefiting plants with nutrients, water, and signaling antibiotic molecules that aid in defense against soil borne harmful pathogens and diseases, while fungi receive metabolites such as carbohydrates in return. The extensive hyphal network between fungi and plants not only enhances nutrient acquisition but also improves soil structure, increasing soil porosity and water-holding capacity, thereby enhancing water absorption by plants, particularly under drought conditions. AMF is associated with the exudation of glomalin protein which is responsible for carbon storage, stress tolerance and soil aggregate stabilization [25]. This aids plants in tolerating diverse environmental stressors and adapting to drought [190]. Fungi act as osmotic regulators in saline environments, assisting plants in adapting and surviving under such conditions. Additionally, they produce compounds that aid in detoxifying heavy metals and pollutants arising from human activities such as pesticide and herbicide use. Lastly, soil fungi are key decomposers of organic matter, breaking down complex organic compounds into simpler forms that plants can absorb as nutrients. This decomposition process releases nutrients, such as nitrogen, phosphorus, and potassium back into the soil, thereby enriching its fertility [30, 190].

5 Factors influencing soil microbial communities

Soil microbial communities play a major role in nutrient cycling and growth and development of plants. Nonetheless, certain factors constantly control their composition, organization, and roles in the soil. Agricultural management systems, soil types, climate change, plant species, and other land management practices can all have an impact on

the microbial populations in the rhizosphere and soil in agroecosystems [198, 199]. Crop rotation practices have been found to affect microbial abundance and diversity in agricultural management systems. For instance, Buyer et al. [198] found that different species of cover crops under rotation with other plants had unique root and shoot effects on soil microbial community composition. Further investigations showed that cropping sequence-induced changes in the soil microbial population had an impact on soil characteristics, suppression of plant pathogens, increased soil microbe enzymes and metabolic activities, and improved crop productivity [26, 27, 200]. Soil microbial populations can be affected by other agricultural practices, such as tillage, synthetic pesticides, and chemical fertilizers. Numerous studies have demonstrated that the use of chemical fertilizers reduces soil bacterial diversity (measured by the Shannon index) compared to the use of compost or manure [201]. In a different study, the continuous use of chemical fertilizer and long-term conventional tillage both considerably changed the composition of the microbial community, but the tillage effect was more extreme [202].

In terms of soil physical properties, the proportions of sand, silt, and clay affect pore space and water retention, which in turn influences microbial habitats [203]. Additionally, the aggregation of soil particles affects aeration and water movement, impacting microbial activity and diversity [204]. Furthermore, availability of water (soil water content) is crucial for microbial metabolic activities and influences the distribution and activity of microorganisms in soil [205]. Soil temperature has an impact on the metabolic rates and composition of microbial communities. Extreme temperatures affect the enzymatic activities of soil-dwelling microorganisms, altering their roles [206].

The availability of nutrients and the general composition of the microbial population are influenced by soil chemical properties, such as pH. While certain microbial species prefer differing pH level, for example, PSB may live in acidic or alkaline environments, the majority of microorganisms require an ideal pH between 6.0 and 7.0 [207]. The presence of essential nutrients in the soil, such as nitrogen, phosphorus, and potassium, are critical for microbial growth and activity. Organic matter provides carbon sources for microbial metabolism and influences soil community composition [208]. Saline and hypersaline environments host a vast array of prokaryotes, including bacteria and archaea. These microorganisms have adapted to thrive under high salt concentrations and elevated osmotic pressure [209].

An example of how these factors influence the activity and efficacy of PSB is dependent on many factors. The ability of PSB to convert insoluble phosphorus into soluble forms is due to the soil's nutrient richness, the bacteria's physiological capabilities, and their growth status. PSB tend to solubilize phosphate in soils under varying environmental conditions influenced by biotic and abiotic factors, such as soil acidity and alkalinity, salinity, nutrient levels, temperature, soil water content, soil type and texture, organic matter content, and human agricultural practices [210]. Studies on the impact of temperature on bacteria in phosphorus solubilization have been unreliable because most reported temperature information differs [22, 211]. For example, many studies have observed that majority of PSB at temperatures between 20 and 30 °C [22, 212–215] while others have documented between 30 °C and 40 °C [216, 217]. PSB also solubilizes phosphorus in areas with extreme temperatures [157, 218, 219].

Microbial interactions in soil coupled by vegetation cover and ecological conditions, land use, plant types and organic matter, and soil pH are all factors influencing the solubilization of P [22, 220, 221]. Hot humid climates solubilize phosphorus more quickly, whereas cool dry climates solubilize phosphorus more slowly. Compared to saturated wet soil, a well-aerated soil would allow for faster phosphorus solubilization [222]. In terms of pH, PSB tolerate both acidic soil using acid phosphatase and alkaline soils using alkaline phosphates, as well as optimal soil pH [223].

Factors influencing the roles, population, community structure, and distribution of fungi in soil include land management practices such as tillage, crop rotation, agroforestry and the use of organic or inorganic fertilizers, herbicides, and pesticides [10, 27, 202]. Additionally, general climate change affects fungi through variations in temperature, soil pH, and nutrient availability, leading to physiological changes in soil habitats [190]. Soil fungi have a significant influence on soil health, environmental sustainability, agricultural productivity, horticulture, and forestry. Furthermore, they indirectly contribute to plant physiology by influencing plant hormone levels and gene expression, leading to changes in plant growth and development, and increased yields, benefiting both humans and animals. More research is needed to determine optimal methods for preserving fungal biodiversity in soil, considering their roles and ecosystem services, such as disease control, pollution detection, and bioremediation [224].

Finally, the functions of soil microorganisms can be influenced by genetic factors. The genetic composition of microbial populations determines their metabolic capability and adaptability to environmental conditions. Genetic phenomena such as horizontal gene transfer, which involves the exchange of genetic material between microorganisms, can introduce new traits and impact community dynamics [225]. This process is common in bacteria that possess mobile genetic elements such as plasmids, transposons, and bacteriophages that facilitate genetic conjugation, transformation, and transduction. Evidence of horizontal gene transfer has been observed in symbiosis genes within and between *Rhizobia*

genera [226]. Environmental stressors, including the presence of toxic heavy metals, pesticides, and other pollutants in the soil, can lead to antibiotic resistance, metabolic changes, or increased virulence in microorganisms, thereby affecting the structure and function of the microbial community [221].

6 Knowledge gaps and prospects for research

Most research on applied microbiology, coupled with advanced molecular techniques, has laid a good foundation for exploiting the potential of the soil microbiome for sustainable agriculture. To build on this foundation, much research is needed to fully understand microbial diversity, interactions, and translation of laboratory findings to field applications. The key research gaps are as follows:

6.1 Microbial diversity and functions

Soil is a critical habitat for complex species (culturable and unculturable) of microbial communities, most of which are yet to be studied. Therefore, there is a need for a comprehensive understanding of the functional diversity of communities within diverse soil types and ecosystems. Advances in DNA sequencing platforms and methodologies such as metagenomics, metabolomics and transcriptomics will reveal functional diversity up to gene level within communities [31, 227–229]. Whole genome shotgun metagenomics sequences all the genetic material in a sample to analyze the collective genomes of the microbial community, whereas amplicon sequencing or metabarcoding approaches target specific marker genes, such as 16S rRNA for bacteria and archaea, or ITS and 18S regions for fungi, to study particular groups of microorganisms [229, 230].

6.2 Molecular mechanisms of microbial interactions

Although several molecular mechanisms of microbial communities are known, we are still far from fully understanding how microbes interact with each other and with plants in different agroecological systems. Agricultural production systems differ in terms of climate from tropical, dry, temperate, continental, polar, and high mountain (alpine) regions and different agricultural management practices, such as organic farming, crop rotations, agro-forestry, and cover cropping. A comprehensive indulgence of how microbes communicate, compete, adapt, or cooperate in diverse ecosystems using molecular mechanisms can help fine-tune agricultural practices that foster beneficial interactions in certain soils and climatic environments [25, 231]. Furthermore, particularly in developing countries, scientific evidence of the contribution of microbial communities to diverse food production systems is still limited. Therefore, more evidence is needed regarding the benefits of biological inputs over synthetic inputs or their synergetic effects.

6.3 Long-term effects of agricultural practices on microbial communities

Sustainable agriculture is shifting towards regenerative and conservation agriculture using resilient agricultural practices that favor soil health and crop productivity. These practices involve the use of reduced tillage systems, crop rotations, animal integration, cover crops, and crop diversity. There are limited studies on the roles of soil microbes in these systems and their impact, especially in developing countries. Additionally, there is limited long-term data on how these practices, such as reduced chemical inputs, crop rotation, and the use of bio-based fertilizers compared with conventional agricultural practices, affect soil microbial communities over decades. Similarly, there is limited understanding of how synthetic inputs, such as pesticides, herbicides, and chemical fertilizers, affect soil microbial diversity and functionality in the long term. Long-term data will help in understanding cumulative microbial dynamics over time [232].

6.4 Genetic manipulation and modification of microbial communities

Although some research has been conducted on the genetic manipulation and engineering of soil microbes, we are still far from fully harnessing these tools for practical applications in soil microbial management. Recent genetic engineering advancements hold potential for in situ control of microbial community composition, transforming the functionality

of existing microbiomes. A notable example is strain-specific CRISPR, which was developed to modify the composition of microbiome communities by selectively purifying or eliminating specific members of a synthetic host collection [233]. The CRISPR-Cas9 system enables rapid targeted genomic alterations in individual cells or organisms. It allows for genome-wide screening, epigenome modifications, transcription regulation, and chromosome imaging. In soil microbes, CRISPR-Cas9 systems can edit specific genes, facilitating the study of gene function and the development of beneficial traits such as availing of nutrients or disease resistance [234–236].

6.5 Microbial contributions to carbon sequestration

The global organic carbon contained in prokaryotes alone is comparable to that in plants [237]. Therefore, soil microbes are critical for soil carbon storage. This is achieved by breaking down organic matter and contributing to the formation of stable organic compounds. Although soil microbes are also involved in soil respiration, which leads to the release of greenhouse gases, these forms are immediately balanced by other microbial metabolic activities such as methanotrophs consuming methane produced through methanogenesis process in soils [238]. The long-term stabilization, carbon cycling, and metabolic pathways of these forms of carbon remain uncertain and poorly understood. The impact of climate change on microbial communities, particularly their ability to adapt to shifts in temperature and moisture, is also not fully understood. Research into the processes, mechanisms, and driving factors of soil microbial carbon dynamics and how microbes are involved, is crucial for understanding carbon sequestration and effectively addressing the growing challenges of climate change [239].

6.6 Scaling microbial solutions

The effectiveness of soil microbes isolated and used as inoculants depends on various factors, including the laboratory, greenhouse, and field conditions. While numerous studies have focused on controlled laboratory and greenhouse experiments, less attention has been paid to field trials. A key challenge is the disconnect between these controlled environments and actual field conditions, where factors such as biotic and abiotic stressors, competition with native organisms, and crop diversity affect the adaptability and stability of inoculants, as well as the development of optimal formulations. Therefore, more studies are needed to explore how to maintain the efficacy of microbial inoculants in diverse field conditions and to assess their performance under varying environmental conditions for inoculants already on the market [240]. Scaling microbial products offers a pathway to sustainable agriculture, benefiting economies, ecosystems, and societies. However, to realize these benefits equitably, supportive policies, investments in infrastructure, and educational efforts are essential. Addressing these socio-economic dimensions is critical for the inclusive and sustainable implementation of these technologies.

7 Conclusion

Integrating soil microbes into the sustainable agricultural management systems brings numerous benefits. Soil microorganisms are responsible for the decomposition and mineralization of soil organic matter, cycling of important nutrients such as nitrogen and phosphorus, maintaining and improving soil structure, enhancing water infiltration, retention, and aeration. They also serve as biological control agents for plant pests and diseases. These benefits align with the various Sustainable Development Goals of the United Nations, such as zero hunger, by promoting sustainable food production through resilient agricultural methods. Promoting microbial activity in food production systems reduces reliance on chemical fertilizers and pesticides, which are expensive and harmful to the environment. Additionally, microorganisms contribute to global biodiversity, support other soil organisms by generating byproducts that enhance their lives, and play a key role in climate change mitigation through carbon stabilization in soils. However, various gaps remain in fully understanding and harnessing the potential of soil microbiomes to transform agriculture toward sustainability. Therefore, future research should prioritize the use of advanced technologies to unravel microbial diversity, and gain deeper insights into their functionality, as these are essential for understanding their interactions with plants. Priority should also be given to translating insights from controlled environments to field conditions, where the services of microbial communities are most needed. This approach will provide a comprehensive understanding of the impacts of management

practices while addressing challenges related to biotic and abiotic stressors, competition with native organisms, the adaptability and stability of inoculants, and the development of optimal formulations for efficacy in agricultural sustainability. Such knowledge is important for exploring methods to maintain the efficacy of microbial inoculants under diverse field conditions.

Acknowledgements Not applicable.

Author contributions K.K: Conceptualizing, Investigation, Data curation & writing of original draft. E.K.M & C.W: Resources, Writing, Supervision, Review & Editing. T.N: Writing, Formal analysis & Data collection. J.M, D.O & D.O: Resources, Review & Supervision. H.M, S.M & J.T: Technical support and proofreads.

Funding There was no funding allocated for this research.

Availability of data and materials No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

1. Coleman D, Callahan M, Jr C. Fundamentals of Soil Ecology: Third Edition. Fundamentals of Soil Ecology: Third Edition. 2017.
2. Rasche F, Knapp D, Kaiser C, Koranda M, Kitzler B, Zechmeister-Boltenstern S, et al. Seasonality and resource availability control bacterial and archaeal communities in soils of a temperate beech forest. *ISME J*. 2011;5:389–402.
3. Muema EK, Cadisch G, Röhl C, Vanlauwe B, Rasche F. Response of ammonia-oxidizing bacteria and archaea to biochemical quality of organic inputs combined with mineral nitrogen fertilizer in an arable soil. *Appl Soil Ecol*. 2015;95:128–39.
4. Rasche F, Musyoki MK, Röhl C, Muema EK, Vanlauwe B, Cadisch G. Lasting influence of biochemically contrasting organic inputs on abundance and community structure of total and proteolytic bacteria in tropical soils. *Soil Biol Biochem*. 2014;74:204–13.
5. Muema EK, Steenkamp ET, Venter SN. Rhizosphere Diazotrophs and other bacteria associated with native and encroaching legumes in the Succulent Karoo Biome in South Africa. *Microorganisms*. 2022;10:216.
6. Wekesa CS, Furch ACU, Oelmüller R. Isolation and characterization of high-efficiency rhizobia from western kenya nodulating with common bean. *Front Microbiol*. 2021;12: 697567.
7. Kiprotich K, Muoma J, Omayio DO, Ndombi TS, Wekesa C. Molecular characterization and mineralizing potential of phosphorus solubilizing bacteria colonizing common bean (*Phaseolus vulgaris* L.) rhizosphere in Western Kenya. *Int J Microbiol*. 2023;2023:6668097.
8. Tian J, Ge F, Zhang D, Deng S, Liu X. Roles of phosphate solubilizing microorganisms from managing soil phosphorus deficiency to mediating biogeochemical P cycle. *Biology (Basel)*. 2021;10:158.
9. Cosme M. Mycorrhizas drive the evolution of plant adaptation to drought. *Commun Biol*. 2023;6:1–10.
10. Singh M, Chauhan A, Srivastava DK, Singh PK. Unveiling arbuscular mycorrhizal fungi: the hidden heroes of soil to control the plant pathogens. *Arch Phytopathol Plant Protection*. 2024;57:427–57. <https://doi.org/10.1080/03235408.2024.2368112>.
11. Ferris H. Contribution of nematodes to the structure and function of the soil food web. *J Nematol*. 2010;42:63–7.
12. Cho H, Kim M, Tripathi B, Adams J. Changes in soil fungal community structure with increasing disturbance frequency. *Microb Ecol*. 2017;74:62–77. <https://doi.org/10.1007/s00248-016-0919-1>.
13. Li Y, Wu J, Chen H. Nematodes as bioindicator of soil health: methods and applications. *Chen J Ying Yong Sheng Tai Xue Bao*. 2005;16:1541–6.
14. Bongers T, Ferris H. Nematode community structure as a bioindicator in environmental monitoring. *Trends Ecol Evol*. 1999;14:224–8.
15. Ali MA, Ahmed T, Wu W, Hossain A, Hafeez R, Islam Masum MM, et al. Advancements in plant and microbe-based synthesis of metallic nanoparticles and their antimicrobial activity against plant pathogens. *Nanomaterials*. 2020;10:1146.
16. Dimopoulou A, Theologidis I, Benaki D, Koukounia M, Zervakou A, Tzima A, et al. Direct antibiotic activity of bacillibactin broadens the biocontrol range of *Bacillus amyloliquefaciens* MBI600. *mSphere*. 2021. <https://doi.org/10.1128/msphere.00376-21>.
17. Du W, Yao Z, Li J, Sun C, Xia J, Wang B, et al. Diversity and antimicrobial activity of endophytic fungi isolated from *Securinega suffruticosa* in the Yellow River Delta. *PLoS ONE*. 2020;15:e0229589. <https://doi.org/10.1371/journal.pone.0229589>.

18. Dastogeer KMG, Zahan MSTI, Rhaman MS, Sarker MSA, Chakraborty A. Microbe-mediated thermotolerance in plants and pertinent mechanisms- a meta-analysis and review. *Front Microbiol.* 2022;13:833566.
19. Wong CKF. Application of microbes in climate-resilient crops. In: Inamuddin, Ahamed MI, Prasad R, editors. *Application of microbes in environmental and microbial biotechnology.* Singapore: Springer Nature; 2022. p. 93–112.
20. Yadav AN, Kour D, Kaur T, Devi R, Yadav A, Dikilitas M, et al. Biodiversity, and biotechnological contribution of beneficial soil microbiomes for nutrient cycling, plant growth improvement and nutrient uptake. *Biocatalysis Agric Biotechnol.* 2021;33:102009.
21. Sharma SB, Sayyed RZ, Trivedi MH, Gobi TA. Phosphate solubilizing microbes: sustainable approach for managing phosphorus deficiency in agricultural soils. *Springerplus.* 2013;2:587.
22. Alori ET, Glick BR, Babalola OO. Microbial phosphorus solubilization and its potential for use in sustainable agriculture. *Front Microbiol.* 2017. <https://doi.org/10.3389/fmicb.2017.00971/full>.
23. Dobrovolskaya TG, Zvyagintsev DG, Chernov IY, Golovchenko AV, Zenova GM, Lysak LV, et al. The role of microorganisms in the ecological functions of soils. *Eurasian Soil Sci.* 2015;48:959–67. <https://doi.org/10.1134/S1064229315090033>.
24. Soumare A, Diedhiou AG, Thuita M, Hafidi M, Ouhdouch Y, Gopalakrishnan S, et al. Exploiting biological nitrogen fixation: a route towards a sustainable agriculture. *Plants (Basel).* 2020;9:1011.
25. Singh PK, Singh M, Tripathi BN. Glomalin: an arbuscular mycorrhizal fungal soil protein. *Protoplasma.* 2013;250:663–9. <https://doi.org/10.1007/s00709-012-0453-z>.
26. Yang T, Evans B, Bainard LD. Pulse frequency in crop rotations alters soil microbial community networks and the relative abundance of fungal plant pathogens. *Front Microbiol.* 2021. <https://doi.org/10.3389/fmicb.2021.667394/full>.
27. D'Acunto L, Andrade JF, Poggio SL, Semmartin M. Diversifying crop rotation increased metabolic soil diversity and activity of the microbial community. *Agric Ecosyst Environ.* 2018;257:159. Available from: https://www.academia.edu/100064319/Diversifying_crop_rotation_increased_metabolic_soil_diversity_and_activity_of_the_microbial_community.
28. Frøslev TG, Nielsen IB, Santos SS, Barnes CJ, Bruun HH, Ejrnæs R. The biodiversity effect of reduced tillage on soil microbiota. *Ambio.* 2022;51:1022–33.
29. Bonaterra A, Badosa E, Daranas N, Francés J, Roselló G, Montesinos E. Bacteria as biological control agents of plant diseases. *Microorganisms.* 2022;10:1759.
30. Nkongolo KK, Narendrula-Kotha R. Advances in monitoring soil microbial community dynamic and function. *J Appl Genetics.* 2020;61:249–63. <https://doi.org/10.1007/s13353-020-00549-5>.
31. Bertola M, Ferrarini A, Visioli G. Improvement of soil microbial diversity through sustainable agricultural practices and its evaluation by -omics approaches: a perspective for the environment, food quality and human safety. *Microorganisms.* 2021;9:1400.
32. Kumar J, Singh D, Ghosh P, Kumar A. Endophytic and epiphytic modes of microbial interactions and benefits. In: Singh DP, Singh HB, Prabha R, editors. *Plant-microbe interactions in agro-ecological perspectives: fundamental mechanisms, methods and functions.* Singapore: Springer; 2017. p. 227–53. https://doi.org/10.1007/978-981-10-5813-4_12.
33. Hakim S, Naqqash T, Nawaz MS, Laraib I, Siddique MJ, Zia R, et al. Rhizosphere engineering with plant growth-promoting microorganisms for agriculture and ecological sustainability. *Front Sustain Food Syst.* 2021. <https://doi.org/10.3389/fsufs.2021.617157>.
34. Hirel B, Tétu T, Lea PJ, Dubois F. Improving nitrogen use efficiency in crops for sustainable agriculture. *Sustainability.* 2011;3:1452–85.
35. Kafeel U, Jahan U, Khan FA. Chapter five—role of mineral nutrients in biological nitrogen fixation. In: Aftab T, Hakeem KR, editors. *Sustainable Plant Nutrition.* Academic Press; 2023 [cited 2024 Jun 5]. p. 87–106. Available from: <https://www.sciencedirect.com/science/article/pii/B9780443186752000043>.
36. Fernández Bidondo L, Silvani V, Colombo RP, Pérgola M, Bompadre M, Godeas A. Pre-symbiotic and symbiotic interactions between *Glomus intraradices* and two *Paenibacillus* species isolated from AM propagules. In vitro and in vivo assays with soybean (AG043RG) as plant host. *Soil Biol Biochem.* 2011;43:1866–72.
37. Moura EG, Carvalho CS, Bucher CPC, Souza JLB, Aguiar ACF, Ferraz Junior ASL, et al. Diversity of rhizobia and importance of their interactions with legume trees for feasibility and sustainability of the tropical agrosystems. *Diversity.* 2020;12:206.
38. Bouznif B, Guefrachi I, Rodríguez de la Vega RC, Hungria M, Mars M, Alunni B, et al. Phylogeography of the Bradyrhizobium spp. Associated With Peanut, *Arachis hypogaea*: fellow travelers or new associations? *Front Microbiol.* 2019. <https://doi.org/10.3389/fmicb.2019.02041/full>.
39. Deicke M, Mohr JF, Roy S, Herzsprung P, Bellenger J-P, Wichard T. Metallophore profiling of nitrogen-fixing *Frankia* spp. to understand metal management in the rhizosphere of actinorhizal plants. *Metallomics.* 2019;11:810–21.
40. Menéndez E, Pérez-Yépez J, Hernández M, Rodríguez-Pérez A, Velázquez E, León-Barrios M. Plant growth promotion abilities of phylogenetically diverse mesorhizobium strains: effect in the root colonization and development of tomato seedlings. *Microorganisms.* 2020;8:412.
41. Temesgen D, Assefa F. Inoculation of native symbiotic effective Sinorhizobium spp. enhanced soybean [*Glycine max* (L.) Merr.] grain yield in Ethiopia. *Environ Syst Res.* 2020;9:38. <https://doi.org/10.1186/s40068-020-00205-1>.
42. Sawana A, Adeolu M, Gupta RS. Molecular signatures and phylogenomic analysis of the genus *Burkholderia*: proposal for division of this genus into the emended genus *Burkholderia* containing pathogenic organisms and a new genus *Paraburkholderia* gen. nov. harboring environmental species. *Front Genet.* 2014;5:429.
43. Kanso S, Patel BKC. *Microvirga subterranea* gen. nov., sp. Nov., a moderate thermophile from a deep subsurface Australian thermal aquifer. *Int J Syst Evol Microbiol.* 2003;53:401–6.
44. Patt TE, Cole GC, Hanson RS. *Methylobacterium*, a New Genus of Facultatively Methylophilic Bacteria. *Int J Syst Bacteriol.* 1976;26:226–9. <https://doi.org/10.1099/00207713-26-2-226>.
45. Demtröder L, Narberhaus F, Masepohl B. Coordinated regulation of nitrogen fixation and molybdate transport by molybdenum. *Mol Microbiol.* 2019;111:17–30.
46. Streicher SL, Valentine RC. The nitrogen fixation (*NIF*) operon(S) of *Klebsiella pneumoniae*. In: Neilands JB, editor. *Microbial iron metabolism.* Academic Press; 1974. p. 211–29.
47. Sumbul A, Ansari RA, Rizvi R, Mahmood I. *Azotobacter*: a potential bio-fertilizer for soil and plant health management. *Saudi J Biol Sci.* 2020;27:3634–40.

48. Zehr JP. Nitrogen fixation by marine cyanobacteria. *Trends Microbiol.* 2011;19:162–73.
49. Masuda Y, Satoh S, Miyamoto R, Takano R, Ishii K, Ohba H, et al. Biological nitrogen fixation in the long-term nitrogen-fertilized and unfertilized paddy fields, with special reference to diazotrophic iron-reducing bacteria. *Arch Microbiol.* 2023;205:291.
50. Tang R, Yang S, Narsing Rao MP, Xie C-J, Han S, Yang Q-E, et al. Three Fe(III)-reducing and nitrogen-fixing bacteria, *Anaeromyxobacter ter-rae* sp. nov., *Anaeromyxobacter oryzae* sp. nov. and *Anaeromyxobacter soli* sp. nov., isolated from paddy soil. *Int J Syst Evol Microbiol.* 2024;74.
51. Masuda Y, Yamanaka H, Xu Z-X, Shiratori Y, Aono T, Amachi S, et al. Diazotrophic anaeromyxobacter isolates from soils. *Appl Environ Microbiol.* 2020;86:e00956-e1020.
52. Cruz-Hernández MA, Mendoza-Herrera A, Bocanegra-García V, Rivera G. *Azospirillum* spp. from plant growth-promoting bacteria to their use in bioremediation. *Microorganisms.* 2022;10:1057.
53. Dong H, Liu W, Zhang H, Wang Z, Feng F, Zhou L, et al. Enhanced biomass production and wastewater treatment in attached co-culture of *Chlorella pyrenoidosa* with nitrogen-fixing bacteria *Azotobacter beijerinckii*. *Bioprocess Biosyst Eng.* 2023;46:707–16.
54. Chen S-L, Tsai M-K, Huang Y-M, Huang C-H. Diversity and characterization of *Azotobacter* isolates obtained from rice rhizosphere soils in Taiwan. *Ann Microbiol.* 2018;68:17–26. <https://doi.org/10.1007/s13213-017-1312-0>.
55. Zhou L, Liu W, Duan H, Dong H, Li J, Zhang S, et al. Improved effects of combined application of nitrogen-fixing bacteria *Azotobacter beijerinckii* and microalgae *Chlorella pyrenoidosa* on wheat growth and saline-alkali soil quality. *Chemosphere.* 2023;313:137409. <https://doi.org/10.1016/j.chemosphere.2022.137409>.
56. Wang S, Xu Z, Xu X, Gao F, Zhang K, Zhang X, et al. Effects of two strains of thermophilic nitrogen-fixing bacteria on nitrogen loss mitigation in cow dung compost. *Bioresour Technol.* 2024;400:130681.
57. Ouyang B, Liu F, Liang C, Zhang J, Hu R, Yuan H, et al. Toxicity and activity inhibition of metal-organic framework MOF-199 to nitrogen-fixing bacterium *Azotobacter vinelandii*. *Sci Total Environ.* 2022;813:151912.
58. Mahapatra S, Yadav R, Ramakrishna W. *Bacillus subtilis* impact on plant growth, soil health and environment: Dr. Jekyll and Mr. Hyde. *J Appl Microbiol.* 2022;132:3543–62. <https://doi.org/10.1111/jam.15480>.
59. Alaswad AA, Oehrlé NW, Krishnan HB. Classical Soybean (*Glycine max* (L.) Merr) Symbionts, *Sinorhizobium fredii* USDA191 and *Bradyrhizobium diazoefficiens* USDA110, reveal contrasting symbiotic phenotype on pigeon pea (*Cajanus cajan* (L.) Millsp.). *Int J Mol Sci.* 2019;20:1091.
60. Rufini M, Oliveira DP, Trochmann A, Soares BL, Andrade MJB de, Moreira FM de S. *Bradyrhizobium* spp. Strains in Symbiosis with Pigeon Pea cv. *Fava-Larga* under Greenhouse and Field Conditions. *Rev Bras Ciênc Solo.* 2016;40:e0160156. Available from: <https://www.scielo.br/j/rbcs/a/7yHXV4chpzRmSPvpCY8DjGm/?lang=en>.
61. Jarecki W. Soybean response to seed inoculation or coating with *Bradyrhizobium japonicum* and foliar fertilization with molybdenum. *Plants.* 2023;12:2431.
62. Scott A, Topp E, Revellin C, Hartmann A, Fruci M. Complete genome sequence of *Bradyrhizobium ottawaense* strain MIAE 01942 isolated from soybean nodules grown in antibiotic-amended soil. *Microbiol Resour Announcements.* 2024;13:e00004-24. <https://doi.org/10.1128/mra.00004-24>.
63. Wasai-Hara S, Itakura M, Fernandes Siqueira A, Takemoto D, Sugawara M, Mitsui H, et al. *Bradyrhizobium ottawaense* efficiently reduces nitrous oxide through high *nosZ* gene expression. *Sci Rep.* 2023;13:18862.
64. Berza Beyene B, Pagano MC, Vaiyapuri RP, Assefa Tuji F. Microbial consortia inoculation of woody legume *Erythrina brucei* increases nodulation and shoot nitrogen and phosphorus under greenhouse conditions. *Biotechnol Rep.* 2022;33:e00707.
65. Tiwari R, Howieson J, Yates R, Tian R, Tapia R, et al. Genome sequence of *Bradyrhizobium* sp. WSM1253; a microsymbiont of *Ornithopus compressus* from the Greek Island of Sifnos. *Stand Genomic Sci.* 2015;10:113. <https://doi.org/10.1186/s40793-015-0115-9>.
66. Bromfield ESP, Cloutier S, Nguyen HDT. Description and complete genome sequences of *Bradyrhizobium symbiodeficiens* sp. Nov., a non-symbiotic bacterium associated with legumes native to Canada. *Int J Syst Evol Microbiol.* 2020;70:442–9. <https://doi.org/10.1099/ijsem.0.003772>.
67. Osei O, Abaidoo RC, Ahiabor BDK, Boddey RM, Rouws LFM. Bacteria related to *Bradyrhizobium yuanmingense* from Ghana are effective groundnut micro-symbionts. *Appl Soil Ecol.* 2018;127:41–50.
68. Bullergahn VB, Menezes KMS, Veloso TGR, da Luz JMR, Castanheira LF, Pereira LL, et al. Diversity of potential nitrogen-fixing bacteria from rhizosphere of the *Coffea arabica* L. and *Coffea canephora* L. *3 Biotech.* 2024;14:27. <https://doi.org/10.1007/s13205-023-03875-7>.
69. Janaki M, Kirupanatha-Rajan P, Senthil-Nathan S, Stanley-Raja V, Al Farraj DA, Aljeidi RA, et al. Beneficial role of *Burkholderia cepacia* in heavy metal bioremediation in metal-polluted soils and enhance the tomato plant growth. *Biocatalysis Agric Biotechnol.* 2024;57:103032.
70. Shahid M, Khan MS. Glyphosate induced toxicity to chickpea plants and stress alleviation by herbicide tolerant phosphate solubilizing *Burkholderia cepacia* PSBB1 carrying multifarious plant growth promoting activities. *3 Biotech.* 2018;8:131.
71. Eren Eroğlu AE, Eroğlu V, Yaşa İ. Genomic insights into the symbiotic and plant growth-promoting traits of “Candidatus Phyllobacterium onerii” sp. Nov. isolated from endemic *Astragalus flavescens*. *Microorganisms.* 2024;12:336.
72. Garau G, Terpolilli J, Hill Y, Tian R, Howieson J, Bräu L, et al. Genome sequence of *Ensifer medicae* Di28; an effective N₂-fixing microsymbiont of *Medicago murex* and *M. polymorpha*. *Stand Genomic Sci.* 2014;9:4. <https://doi.org/10.1186/1944-3277-9-4>.
73. Reeve W, Chain P, O’Hara G, Ardley J, Nandesena K, Bräu L, et al. Complete genome sequence of the *Medicago* microsymbiont *Ensifer* (*Sinorhizobium*) *medicae* strain WSM419. *Stand Genomic Sci.* 2010;2:77–86.
74. Terpolilli J, Hill Y, Tian R, Howieson J, Bräu L, Goodwin L, et al. Genome sequence of *Ensifer meliloti* strain WSM1022; a highly effective microsymbiont of the model legume *Medicago truncatula* A17. *Stand Genomic Sci.* 2013;9:315–24. <https://doi.org/10.4056/sigs.4608286>.
75. Qin Y, Huang Y-Y, Khan Q, Zhang K-K, Guo D-J, Yang L-T, et al. Cloning, prokaryotic expression and functional characterization of *NifH* gene from the associative nitrogen-fixing bacteria *Klebsiella Variicola* DX120E. *Iran J Biotechnol.* 2023;21:89–99.
76. Chen Y, Huang Z, Li J, Su G, Feng B. Complete genome sequence of *Kosakonia radincincitans* GXGL-4A, a nitrogen-fixing bacterium with capability to degrade TEX. *Curr Microbiol.* 2020;77:1848–57. <https://doi.org/10.1007/s00284-020-01942-3>.
77. Gunnabo AH, van Heerwaarden J, Geurts R, Wolde-meskel E, Degefu T, Giller KE. Symbiotic interactions between chickpea (*Cicer arietinum* L.) genotypes and *Mesorhizobium* strains. *Symbiosis.* 2020;82:235–48. <https://doi.org/10.1007/s13199-020-00724-6>.

78. Wanjofu EI, Venter SN, Beukes CW, Steenkamp ET, Gwata ET, Muema EK. Nodulation and growth promotion of chickpea by mesorhizobium isolates from diverse sources. *Microorganisms*. 2022;10:2467.
79. Gao M, Yang H, Zhao J, Liu J, Sun Y, Wang Y, et al. *Paenibacillus brassicae* sp. Nov., isolated from cabbage rhizosphere in Beijing, China. *Antonie Van Leeuwenhoek*. 2013;103:647–53. <https://doi.org/10.1007/s10482-012-9849-1>.
80. Wang L-Y, Li J, Li QX, Chen S-F. *Paenibacillus beijingensis* sp. Nov., a nitrogen-fixing species isolated from wheat rhizosphere soil. *Antonie Van Leeuwenhoek*. 2013;104:675–83. <https://doi.org/10.1007/s10482-013-9974-5>.
81. Chen X-R, Shao C-B, Wang Y-W, He M-X, Ma K-D, Wang H-M, et al. *Paenibacillusvini* sp. nov., isolated from alcohol fermentation pit mud in Sichuan Province, China. *Antonie Van Leeuwenhoek*. 2015;107:1429–36. <https://doi.org/10.1007/s10482-015-0438-y>.
82. Ke X, Feng S, Wang J, Lu W, Zhang W, Chen M, et al. Effect of inoculation with nitrogen-fixing bacterium *Pseudomonas stutzeri* A1501 on maize plant growth and the microbiome indigenous to the rhizosphere. *Syst Appl Microbiol*. 2019;42:248–60.
83. Huang Q, Feng Y, Shan H-W, Chen J-P, Wu W. A Novel nitrogen-fixing bacterium *Raoultella electrica* isolated from the midgut of the leafhopper *Recilia dorsalis*. *Insects*. 2023;14:431.
84. Zhang YJ, Zheng WT, Everall I, Young JPW, Zhang XX, Tian CF, et al. *Rhizobium anhuiense* sp. Nov., isolated from effective nodules of *Vicia faba* and *Pisum sativum*. *Int J Syst Evol Microbiol*. 2015;65:2960–7.
85. Aguilar OM, Collavino MM, Mancini U. Nodulation competitiveness and diversification of symbiosis genes in common beans from the American centers of domestication. *Sci Rep*. 2022;12:4591.
86. Silva C, Vinuesa P, Eguiarte LE, Martínez-Romero E, Souza V. *Rhizobium etli* and *Rhizobium gallicum* Nodulate common bean (*Phaseolus vulgaris*) in a traditionally managed milpa plot in Mexico: population genetics and biogeographic implications. *Appl Environ Microbiol*. 2003;69:884–93.
87. Hawkins JP, Ordóñez PA, Oresnik IJ. Complete genome sequences of *Rhizobium gallicum* M101 and two potential new rhizobium species isolated from soils in central Canada. *Microbiol Resour Announcements*. 2022;11:e00216–e222. <https://doi.org/10.1128/mra.00216-22>.
88. Sharma A, Bandamaravuri KB, Sharma A, Arora DK. Phenotypic and molecular assessment of chickpea rhizobia from different chickpea cultivars of India. *3 Biotech*. 2017;7:327. <https://doi.org/10.1007/s13205-017-0952-x>.
89. Chaudhary T, Gera R, Shukla P. Deciphering the potential of *Rhizobium pusense* MB-17a, a plant growth-promoting root endophyte, and functional annotation of the genes involved in the metabolic pathway. *Front Bioeng Biotechnol*. 2021. <https://doi.org/10.3389/fbioe.2020.617034>.
90. Mir MI, Kumar BK, Gopalakrishnan S, Vadlamudi S, Hameeda B. Characterization of rhizobia isolated from leguminous plants and their impact on the growth of ICCV 2 variety of chickpea (*Cicer arietinum* L.). *Heliyon*. 2021;7. Available from: [https://www.cell.com/heliyon/abstract/S2405-8440\(21\)02424-5](https://www.cell.com/heliyon/abstract/S2405-8440(21)02424-5).
91. Irisarri P, Cardozo G, Tartaglia C, Reyno R, Gutiérrez P, Lattanzi FA, et al. Selection of competitive and efficient rhizobia strains for white clover. *Front Microbiol*. 2019. <https://doi.org/10.3389/fmicb.2019.00768/full>.
92. Sablok G, Rosselli R, Seeman T, van Velzen R, Polone E, Giacomini A, et al. Draft genome sequence of the nitrogen-fixing rhizobium *sullae* type strain IS123T focusing on the key genes for symbiosis with its host *Hedysarum coronarium* L. *Front Microbiol*. 2017. <https://doi.org/10.3389/fmicb.2017.01348/full>.
93. Lecona AM, Nanjareddy K, Blanco L, Piazza V, Vera-Núñez JA, Lara M, et al. CRK12: a key player in regulating the *Phaseolus vulgaris*-*Rhizobium tropici* symbiotic interaction. *Int J Mol Sci*. 2023;24:11720.
94. Messias M, Asobia PC, de Brito Ferreira EP. Economic analysis of rhizobia and azospirilla co-inoculation in common beans. *Bull Natl Res Centre*. 2023;47:173. <https://doi.org/10.1186/s42269-023-01149-z>.
95. Temprano-Vera F, Rodríguez-Navarro DN, Acosta-Jurado S, Perret X, Fossou RK, Navarro-Gómez P, et al. *Sinorhizobium fredii* strains HH103 and NGR234 form nitrogen fixing nodules with diverse wild soybeans (*Glycine soja*) from central china but are ineffective on Northern China accessions. *Front Microbiol*. 2018. <https://doi.org/10.3389/fmicb.2018.02843/full>.
96. Wang J, Jia Y, Whalen JK, McShane H, Driscoll BT, Sunahara GI. Evidence that nano-TiO₂ induces acute cytotoxicity to the agronomically beneficial nitrogen-fixing bacteria *Sinorhizobium meliloti*. *Can J Microbiol*. 2022;68:67–72. <https://doi.org/10.1139/cjm-2021-0124>.
97. Yang L, El Msehli S, Benyamina S, Lambert A, Hopkins J, Cazareth J, et al. Glutathione deficiency in *Sinorhizobium meliloti* does not impair bacteroid differentiation but induces early senescence in the interaction with *Medicago truncatula*. *Front Plant Sci*. 2020. <https://doi.org/10.3389/fpls.2020.00137/full>.
98. Martinsda Costa E, Almeida Ribeiro PR, Soaresde Carvalho T, Pereira Vicentin R, Balsanelli E, Maltempide Souza E, et al. Efficient nitrogen-fixing bacteria isolated from soybean nodules in the semi-arid region of northeast Brazil are classified as *Bradyrhizobium brasilense* (*Symbiovar Sojae*). *Curr Microbiol*. 2020;77:1746–55. <https://doi.org/10.1007/s00284-020-01993-6>.
99. Göttfert M. Regulation and function of rhizobial nodulation genes. *FEMS Microbiol Rev*. 1993;10:39–63.
100. Schultze M, Kondorosi A. Regulation of symbiotic root nodule development. *Annu Rev Genet*. 1998;32:33–57.
101. Xiong Q, Hu J, Wei H, Zhang H, Zhu J. Relationship between plant roots, rhizosphere microorganisms, and nitrogen and its special focus on rice. *Agriculture*. 2021;11:234.
102. Einsle O, Rees DC. Structural enzymology of nitrogenase enzymes. *Chem Rev*. 2020;120:4969–5004. <https://doi.org/10.1021/acs.chemrev.0c00067>.
103. Lindström K, Mousavi SA. Effectiveness of nitrogen fixation in rhizobia. *Microbial Biotechnol*. 2020;13:1314–35. <https://doi.org/10.1111/1751-7915.13517>.
104. Singh M, Vyas D, Singh PK. Interaction of soil microbes with mycorrhizal fungi in tomato. *Arch Phytopathol Plant Protection*. 2014;47:737–43. <https://doi.org/10.1080/03235408.2013.820389>.
105. Mahmud K, Makaju S, Ibrahim R, Missaoui A. Current progress in nitrogen fixing plants and microbiome research. *Plants*. 2020;9:97.
106. Dos Santos PC. Molecular biology and genetic engineering in nitrogen fixation. In: Ribbe MW, editor. *Nitrogen fixation: methods and protocols*. Totowa: Humana Press; 2011. p. 81–92. https://doi.org/10.1007/978-1-61779-194-9_6.
107. Güngör B, Biró JB, Domonkos Á, Horváth B, Kaló P. Targeted mutagenesis of *Medicago truncatula* nodule-specific cysteine-rich (NCR) genes using the *Agrobacterium* rhizogenes-mediated CRISPR/Cas9 system. *Sci Rep*. 2023;13:20676.
108. Wang L, Xiao Y, Wei X, Pan J, Duanmu D. Highly efficient CRISPR-mediated base editing in *Sinorhizobium meliloti*. *Front Microbiol*. 2021. <https://doi.org/10.3389/fmicb.2021.686008/full>.

109. Chang W, Yang C, Liu T, Tian P, Zhang S, Dai X, et al. Revealing the phosphate-solubilizing characteristics and mechanisms of the plant growth-promoting bacterium *Agrobacterium deltaense* C1. *J Appl Microbiol*. 2024;135:lxad284. <https://doi.org/10.1093/jambio/lxad284>.
110. Soares AS, Nascimento VL, de Oliveira EE, Jumbo LV, dos Santos GR, Queiroz LL, et al. *Pseudomonas aeruginosa* and *Bacillus cereus* isolated from Brazilian Cerrado soil act as phosphate-solubilizing bacteria. *Curr Microbiol*. 2023;80:146. <https://doi.org/10.1007/s00284-023-03260-w>.
111. de Souza AES, Filla VA, da Silva JPM, Barbosa Júnior MR, de Oliveira-Paiva CA, Coelho AP, et al. Application of *Bacillus* spp. phosphate-solubilizing bacteria improves common bean production compared to conventional fertilization. *Plants*. 2023;12:3827.
112. Alamzeb M, Iqbal A, Inamullah, Iqbal M, Ullah I. Integrated use of phosphorus sources, phosphate solubilizing bacteria, and rhizobium enhanced growth, nitrogen, and phosphorus uptake in chickpea. *J Plant Nutr*. 2024. <https://doi.org/10.1080/01904167.2024.2369086>.
113. Cheng Y, Narayanan M, Shi X, Chen X, Li Z, Ma Y. Phosphate-solubilizing bacteria: their agroecological function and optimistic application for enhancing agro-productivity. *Sci Total Environ*. 2023;901:166468.
114. Du G-X, Qu L-Y, Hong X-G, Li C-H, Ding D-W, Gao P, et al. *Kushneria phosphatilytica* sp. nov., a phosphate-solubilizing bacterium isolated from a solar saltern. *Int J Syst Evol Microbiol*. 2021;71.
115. Li Y, Li Q, Guan G, Chen S. Phosphate solubilizing bacteria stimulate wheat rhizosphere and endosphere biological nitrogen fixation by improving phosphorus content. *PeerJ*. 2020;8: e9062.
116. Cappelletti M, Presentato A, Piacenza E, Firrincieli A, Turner RJ, Zannoni D. Biotechnology of *Rhodococcus* for the production of valuable compounds. *Appl Microbiol Biotechnol*. 2020;104:8567–94. <https://doi.org/10.1007/s00253-020-10861-z>.
117. Musa SI, Beckley I. Screening of bacterial isolates for phosphate solubilizing capability in a ferruginous ultisol in Benin City, Edo State, Nigeria. *Bayero J Pure Appl Sci*. 2021;13:94–106.
118. Lee H, Han JY, Kim D-U. *Sinomonas terrae* sp. nov., isolated from an agricultural soil. *J Microbiol Biotechnol*. 2023;33:909–14.
119. Pan L, Cai B. Phosphate-solubilizing bacteria: advances in their physiology, molecular mechanisms and microbial community effects. *Microorganisms*. 2023;11:2904.
120. Wang Z, Zhang H, Liu L, Li S, Xie J, Xue X, et al. Screening of phosphate-solubilizing bacteria and their abilities of phosphorus solubilization and wheat growth promotion. *BMC Microbiol*. 2022;22:296.
121. Kour D, Rana KL, Sheikh I, Kumar V, Yadav AN, Dhaliwal HS, et al. Alleviation of drought stress and plant growth promotion by *Pseudomonas libanensis* EU-LWNA-33, a drought-adaptive phosphorus-solubilizing bacterium. *Proc Natl Acad Sci, India, Sect B Biol Sci*. 2020;90:785–95. <https://doi.org/10.1007/s40011-019-01151-4>.
122. Ou K, He X, Cai K, Zhao W, Jiang X, Ai W, et al. Phosphate-solubilizing *Pseudomonas* sp. strain WS32 rhizosphere colonization-induced expression changes in wheat roots. *Front Microbiol*. 2022. <https://doi.org/10.3389/fmicb.2022.927889/full>.
123. Zeng Q, Wu X, Wen X. Identification and characterization of the rhizosphere phosphate-solubilizing bacterium *Pseudomonas frederiksbergensis* JW-SD2, and its plant growth-promoting effects on poplar seedlings. *Ann Microbiol*. 2016;66:1343–54. <https://doi.org/10.1007/s13213-016-1220-8>.
124. Singh A, Patani A, Patel M, Vyas S, Verma RK, Amari A, et al. Tomato seed bio-priming with *Pseudomonas aeruginosa* strain PAR: a study on plant growth parameters under sodium fluoride stress. *Front Microbiol*. 2024;14:1330071.
125. Bakki M, Banane B, Marhane O, Esmaeel Q, Hatimi A, Barka EA, et al. Phosphate solubilizing *Pseudomonas* and *Bacillus* combined with rock phosphates promoting tomato growth and reducing bacterial canker disease. *Front Microbiol*. 2024. <https://doi.org/10.3389/fmicb.2024.1289466/full>.
126. Blanco-Vargas A, Rodríguez-Gacha LM, Sánchez-Castro N, Garzón-Jaramillo R, Pedroza-Camacho LD, Poutou-Piñales RA, et al. Phosphate-solubilizing *Pseudomonas* sp., and *Serratia* sp., co-culture for *Allium cepa* L. growth promotion. *Heliyon*. 2020;6:e05218.
127. Das Mohapatra M, Sahoo RK, Tuteja N. Phosphate solubilizing bacteria, *Pseudomonas aeruginosa*, improve the growth and yield of groundnut (*Arachis hypogaea* L.). *Physiol Mol Biol Plants*. 2024;30:1099–111. <https://doi.org/10.1007/s12298-024-01478-x>.
128. Dasila H, Sah VK, Jaggi V, Kumar A, Tewari L, Taj G, et al. Cold-tolerant phosphate-solubilizing *Pseudomonas* strains promote wheat growth and yield by improving soil phosphorus (P) nutrition status. *Front Microbiol*. 2023. <https://doi.org/10.3389/fmicb.2023.1135693/full>.
129. Damo JLC, Shimizu T, Sugiura H, Yamamoto S, Agake S, Anarna J, et al. The application of sulfur influences microbiome of soybean rhizosphere and nutrient-mobilizing bacteria in andosol. *Microorganisms*. 2023;11:1193.
130. Rawat P, Das S, Shankhdhar D, Shankhdhar SC. Phosphate-solubilizing microorganisms: mechanism and their role in phosphate solubilization and uptake. *J Soil Sci Plant Nutr*. 2021;21:49–68. <https://doi.org/10.1007/s42729-020-00342-7>.
131. Linu MS, Asok AK, Thampi M, Sreekumar J, Jisha MS. Plant growth promoting traits of indigenous phosphate solubilizing *Pseudomonas aeruginosa* isolates from Chilli (*Capsicum annum* L.) rhizosphere. *Commun Soil Sci Plant Anal*. 2019;50:444–57. <https://doi.org/10.1080/00103624.2019.1566469>.
132. Li X, Ren X, Ibrahim E, Kong H, Wang M, Xia J, et al. Response of Chinese cabbage (*Brassica rapa* subsp. *pekinensis*) to bacterial soft rot infection by change of soil microbial community in root zone. *Front Microbiol*. 2024. <https://doi.org/10.3389/fmicb.2024.1401896/full>.
133. Chen X, Yang C, Palta JA, Li Y, Fan X. An *Enterobacter cloacae* strain NG-33 that can solubilize phosphate and promote maize growth. *Front Microbiol*. 2022. <https://doi.org/10.3389/fmicb.2022.1047313/full>.
134. Kim KY, Jordan D, McDonald GA. *Enterobacter agglomerans*, phosphate solubilizing bacteria, and microbial activity in soil: effect of carbon sources. *Soil Biol Biochem*. 1998;30:995–1003.
135. Borham A, Belal E, Metwaly M, El-gremy SM. Phosphate Solubilization by *Enterobacter cloacae* and its Impact on Growth and Yield of Wheat Plants. *Journal of Sustainable Agricultural Sciences*. 2017; Available from: https://journals.ekb.eg/article_3805.html.
136. Mendoza-Arroyo GE, Chan-Bacab MJ, Aguila-Ramírez RN, Ortega-Morales BO, Canché Solís RE, Chab-Ruiz AO, et al. Inorganic phosphate solubilization by a novel isolated bacterial strain *Enterobacter* sp. ITCB-09 and its application potential as biofertilizer. *Agriculture*. 2020;10:383.
137. Damo JLC, Pedro M, Sison ML. Phosphate solubilization and plant growth promotion by *Enterobacter* sp. isolate. *Appl Microbiol*. 2024;4:1177–92.

138. Safirzadeh S, Chorom M, Enayatizamir N. Effect of phosphate solubilising bacteria (*Enterobacter cloacae*) on phosphorus uptake efficiency in sugarcane (*Saccharum officinarum* L.). *Soil Res.* 2019;57:333–41. Available from: <https://www.publish.csiro.au/sr/SR18128>.
139. Pantigoso HA, He Y, Manter DK, Fonte SJ, Vivanco JM. Phosphorus-solubilizing bacteria isolated from the rhizosphere of wild potato *Solanum bulbocastanum* enhance growth of modern potato varieties. *Bull Natl Res Cent.* 2022;46:224. <https://doi.org/10.1186/s42269-022-00913-x>.
140. Kang S-M, Khan M-A, Hamayun M, Kim L-R, Kwon E-H, Kang Y-S, et al. Phosphate-solubilizing *Enterobacter ludwigii* AFFR02 and *Bacillus megaterium* Mj1212 rescues Alfalfa's growth under post-drought stress. *Agriculture.* 2021;11:485.
141. Dip DP, Sannazzaro AI, Otondo J, Pistorio M, Estrella MJ. *Enterobacter* and *Pseudomonas*: two dominant players in the rhizosphere phosphate-solubilizing bacterial communities of forage grasses adapted to alkaline-sodic soils of the flooding pampa. 2023. Available from: <https://www.researchsquare.com/article/rs-3538198/v1>.
142. Liu M, Liu X, Cheng B-S, Ma X-L, Lyu X-T, Zhao X-F, et al. Selection and evaluation of phosphate-solubilizing bacteria from grapevine rhizospheres for use as biofertilizers. *Spanish J Agric Res.* 2016;14:e1106–e1106.
143. Jiao L, Cao X, Wang C, Chen F, Zou H, Yue L, et al. Crosstalk between *in situ* root exudates and rhizobacteria to promote rice growth by selenium nanomaterials. *Sci Total Environ.* 2023;878:163175.
144. Liu Z, Xiao J, Zhang X, Dou S, Gao T, Wang D, et al. Influence of *Bacillus subtilis* strain Z-14 on microbial communities of wheat rhizospheric soil infested with *Gaeumannomyces graminis* var. *tritici*. *Front Microbiol.* 2022. <https://doi.org/10.3389/fmicb.2022.923242/full>.
145. Mukhtar S, Shahid I, Mehnaz S, Malik KA. Assessment of two carrier materials for phosphate solubilizing biofertilizers and their effect on growth of wheat (*Triticum aestivum* L.). *Microbiol Res.* 2017;205:107–17.
146. Tahir M, Khalid U, Ijaz M, Shah GM, Naeem MA, Shahid M, et al. Combined application of bio-organic phosphate and phosphorus solubilizing bacteria (*Bacillus* strain MWT 14) improve the performance of bread wheat with low fertilizer input under an arid climate. *Braz J Microbiol.* 2018;49:15–24. Available from: <https://www.scielo.br/j/bjm/a/LYZ7yk7F68pBBMs7MNfj8N/?lang=en&format=html>.
147. Mohamed EAH, Farag AG, Youssef SA. Phosphate solubilization by *Bacillus subtilis* and *Serratia marcescens* isolated from tomato plant rhizosphere. *J Environ Protection.* 2018;9:266–77. Available from: <https://www.scirp.org/journal/paperinformation.aspx?paperid=83367>.
148. Saeid A, Prochownik E, Dobrowolska-Iwanek J. Phosphorus solubilization by bacillus species. *Molecules.* 2018;23:2897.
149. Wang T, Liu M-Q, Li H-X. Inoculation of phosphate-solubilizing bacteria *Bacillus thuringiensis* B1 increases available phosphorus and growth of peanut in acidic soil. *Acta Agric Scand Section B Soil Plant Sci.* 2014;64:252–9. <https://doi.org/10.1080/09064710.2014.905624>.
150. Mažlytė R, Kaziūnienė J, Orola L, Valkovska V, Lastauskienė E, Gegeckas A. Phosphate solubilizing microorganism *Bacillus* sp. MVY-004 and its significance for biomineral fertilizers' development in agrobiotechnology. *Biology.* 2022;11:254.
151. Mahdi I, Fahsi N, Hafidi M, Allaoui A, Biskri L. Plant growth enhancement using rhizospheric halotolerant phosphate solubilizing bacterium *Bacillus licheniformis* QA1 and *Enterobacter asburiae* QF11 isolated from *Chenopodium quinoa* Willd. *Microorganisms.* 2020;8:948.
152. Elkoca E, Kantar F, Sahin F. Influence of nitrogen fixing and phosphorus solubilizing bacteria on the nodulation, plant growth, and yield of chickpea. *J Plant Nutr.* 2007;31:157–71. <https://doi.org/10.1080/01904160701742097>.
153. Pandey P, Maheshwari DK. Bioformulation of *Burkholderia* sp. MSSP with a multispecies consortium for growth promotion of *Cajanus cajan*. *Can J Microbiol.* 2007;53:213–22. <https://doi.org/10.1139/w06-118>.
154. Song O-R, Lee S-J, Lee Y-S, Lee S-C, Kim K-K, Choi Y-L. Solubilization of insoluble inorganic phosphate by *Burkholderia cepacia* DA23 isolated from cultivated soil. *Braz J Microbiol.* 2008;39:151–6. Available from: <https://www.scielo.br/j/bjm/a/8g8JXs5pT5RDqSzWRFGZk4v/?lang=en>.
155. Stephen J, Shabanamol S, Rishad KS, Jisha MS. Growth enhancement of rice (*Oryza sativa*) by phosphate solubilizing *Gluconacetobacter* sp. (MTCC 8368) and *Burkholderia* sp. (MTCC 8369) under greenhouse conditions. *3 Biotech.* 2015;5:831–7. <https://doi.org/10.1007/s13205-015-0286-5>.
156. Moreno-Conn LM, Casallas ML, Barrera FMC. Solubilización de fosfatos por bacterias del género *Burkholderia* aisladas de oxisoles de la altillanura colombiana. *Ciencia y Tecnología Agropecuaria.* 2021;22.
157. Panda MK, Sahu MK, Tayung K. Isolation and characterization of a thermophilic *Bacillus* sp. with protease activity isolated from hot spring of Tarabalo, Odisha, India. *Iran J Microbiol.* 2013;5:159–65.
158. Panda P, Choudhury A, Chakraborty S, Ray D, Deb S, Patra P, et al. Phosphorus solubilizing bacteria from tea soils and their phosphate solubilizing abilities. *Int J Bioresour Sci.* 2017;4:113.
159. Park K-H, Lee O-M, Jung H-I, Jeong J-H, Jeon Y-D, Hwang D-Y, et al. Rapid solubilization of insoluble phosphate by a novel environmental stress-tolerant *Burkholderia vietnamiensis* M6 isolated from ginseng rhizospheric soil. *Appl Microbiol Biotechnol.* 2010;86:947–55. <https://doi.org/10.1007/s00253-009-2388-7>.
160. Gao M, Zhou J, Wang E, Chen Q, Xu J, Sun J. Multiphasic characterization of a plant growth promoting bacterial strain, *Burkholderia* sp. 7016 and its effect on tomato growth in the field. *J Integr Agric.* 2015;14:1855–63.
161. Ibáñez A, Díez-Galán A, Cobos R, Calvo-Peña C, Barreiro C, Medina-Turienzo J, et al. Using rhizosphere phosphate solubilizing bacteria to improve barley (*Hordeum vulgare*) plant productivity. *Microorganisms.* 2021;9:1619.
162. Bhakat K, Chakraborty A, Islam E. Characterization of zinc solubilization potential of arsenic tolerant *Burkholderia* spp. isolated from rice rhizospheric soil. *World J Microbiol Biotechnol.* 2021;37:39. <https://doi.org/10.1007/s11274-021-03003-8>.
163. Shome S, Barman A, Solaiman ZM. Rhizobium and phosphate solubilizing bacteria influence the soil nutrient availability, growth, yield, and quality of soybean. *Agriculture.* 2022;12:1136.
164. Alikhani HA, Saleh-Rastin N, Antoun H. Phosphate solubilization activity of rhizobia native to Iranian soils. In: Velázquez E, Rodríguez-Barrueco C, editors. *First international meeting on microbial phosphate solubilization*. Dordrecht: Springer Netherlands; 2007. p. 35–41.
165. Tairo E. Micronutrients uptake in soybean (*Glycine max* L.) as affected by *Bradyrhizobium japonicum* inoculation and phosphorus (p) supplements. *World J Soil Crop Sci Res.* 2014;1:1–9.
166. Sridevi M, Mallaiha KV. Phosphate solubilization by Rhizobium strains. *Indian J Microbiol.* 2009;49:98–102.
167. Tahir M, Mirza MS, Zaheer A, Dimitrov MR, Smidt H, Hameed S. Isolation and identification of phosphate solubilizer “*Azospirillum*, *Bacillus*” and “*Enterobacter*” strains by 16SrRNA sequence analysis and their effect on growth of wheat (“*Triticum aestivum*” L.). *Aust J Crop Sci.* 2013;7:1284–92. <https://doi.org/10.3316/INFORMIT.619865610861415>.

168. Rodriguez H, Gonzalez T, Goire I, Bashan Y. Gluconic acid production and phosphate solubilization by the plant growth-promoting bacterium *Azospirillum* spp. *Naturwissenschaften*. 2004;91:552–5. <https://doi.org/10.1007/s00114-004-0566-0>.
169. López-Ortega M del P, Criollo-Campos PJ, Gómez-Vargas RM, Camelo-Rusinque M, Estrada-Bonilla G, Garrido-Rubiano MF, et al. Characterization of diazotrophic phosphate solubilizing bacteria as growth promoters of maize plants. *Revista Colombiana de Biotecnología*. 2013 [cited 2024 Sep 27];15:115–23. Available from: http://www.scielo.org.co/scielo.php?script=sci_abstract&pid=S0123-34752013000200014&lng=en&nrm=iso&tlng=en.
170. Borgi MA, Saidi I, Moula A, Rhimi S, Rhimi M. The attractive *Serratia plymuthica* BMA1 strain with high rock phosphate-solubilizing activity and its effect on the growth and phosphorus uptake by *Vicia faba* L. plants. *Geomicrobiol J*. 2020;37:437–45. <https://doi.org/10.1080/01490451.2020.1716892>.
171. Ludueña LM, Anzuay MS, Angelini JG, McIntosh M, Becker A, Rupp O, et al. Strain *Serratia* sp. S119: a potential biofertilizer for peanut and maize and a model bacterium to study phosphate solubilization mechanisms. *Appl Soil Ecol*. 2018;126:107–12.
172. de Lima JD, Monteiro PHR, Rivadavea WR, Barbosa M, Cordeiro RD, Garboggini FF, et al. Potential of endophytic bacteria from *Acacia mearnsii*: phosphate solubilization, indole acetic acid production, and application in wheat. *Appl Soil Ecol*. 2024;196:105315.
173. Rfaki A, Zennouhi O, Aliyat FZ, Nassiri L, Ibjibijen J. Isolation, selection and characterization of root-associated rock phosphate solubilizing bacteria in moroccan wheat (*Triticum aestivum* L.). *Geomicrobiol J*. 2020;37:230–41. <https://doi.org/10.1080/01490451.2019.1694106>.
174. Wani P, Khan M, Zaidi A. Co-inoculation of nitrogen-fixing and phosphate-solubilizing bacteria to promote growth, yield and nutrient uptake in chickpea. 2007 [cited 2024 Sep 27]; Available from: <https://akjournals.com/view/journals/014/55/3/article-p315.xml>.
175. Peix A, Rivas-Boyer AA, Mateos PF, Rodríguez-Barrueco C, Martínez-Molina E, Velazquez E. Growth promotion of chickpea and barley by a phosphate solubilizing strain of *Mesorhizobium mediterraneum* under growth chamber conditions. *Soil Biol Biochem*. 2001;33:103–10.
176. Ramos Cabrera EV, Delgado Espinosa ZY, Solís Pino AF. Use of phosphorus-solubilizing microorganisms as a biotechnological alternative: a review. *Microorganisms*. 2024;12:1591.
177. da Silva LI, Pereira MC, de Carvalho AMX, Buttrós VH, Pasqual M, Dória J. Phosphorus-solubilizing microorganisms: a key to sustainable agriculture. *Agriculture*. 2023;13:462.
178. Pikovskaya R, Pikovskaya R. Mobilization of phosphorus in soil in connection with the vital activity of some microbial species. 1948 [cited 2024 Jun 16]. Available from: <https://www.semanticscholar.org/paper/Mobilization-of-phosphorus-in-soil-in-connection-of-Pikovskaya-Pikovskaya/8e97d2ce9a1f74e027597915f357c0277976f887>.
179. Nautiyal CS. An efficient microbiological growth medium for screening phosphate solubilizing microorganisms. *FEMS Microbiol Lett*. 1999;170:265–70. <https://doi.org/10.1111/j.1574-6968.1999.tb13383.x>.
180. Boubekri K, Soumare A, Mardad I, Lyamlouli K, Hafidi M, Ouhdouch Y, et al. The screening of potassium- and phosphate-solubilizing actinobacteria and the assessment of their ability to promote wheat growth parameters. *Microorganisms*. 2021;9:470.
181. Gupta R, Anshu A, Noureldeen A, Darwish H. Rhizosphere mediated growth enhancement using phosphate solubilizing rhizobacteria and their tri-calcium phosphate solubilization activity under pot culture assays in Rice (*Oryza sativa*). *Saudi J Biol Sci*. 2021;28:3692–700.
182. Yu H, Wu X, Zhang G, Zhou F, Harvey PR, Wang L, et al. Identification of the phosphorus-solubilizing bacteria strain JP233 and its effects on soil phosphorus leaching loss and crop growth. *Front Microbiol*. 2022;13:892533.
183. Pande A, Pandey P, Mehra S, Singh M, Kaushik S. Phenotypic and genotypic characterization of phosphate solubilizing bacteria and their efficiency on the growth of maize. *J Genet Eng Biotechnol*. 2017;15:379–91.
184. Canarini A, Fuchslueger L, Schneckner J, Metzke D, Nelson DB, Kahmen A, et al. Soil fungi remain active and invest in storage compounds during drought independent of future climate conditions. *Nat Commun*. 2024;15:10410.
185. Begum N, Qin C, Ahanger MA, Raza S, Khan MI, Ashraf M, et al. Role of arbuscular mycorrhizal fungi in plant growth regulation: implications in abiotic stress tolerance. *Front Plant Sci*. 2019;10:1068.
186. Wan Mohtar WHM, Wan-Mohtar WAAQI, Zahuri AA, Ibrahim MF, Show P-L, Ilham Z, et al. Role of ascomycete and basidiomycete fungi in meeting established and emerging sustainability opportunities: a review. *Bioengineered*. 2023;13:14903–35.
187. Marro N, Grilli G, Soteras F, Caccia M, Longo S, Cofré N, et al. The effects of arbuscular mycorrhizal fungal species and taxonomic groups on stressed and unstressed plants: a global meta-analysis. *New Phytol*. 2022;235:320–32. <https://doi.org/10.1111/nph.18102>.
188. Pirrello C, Mizzotti C, Tomazetti TC, Colombo M, Bettinelli P, Prodorutti D, et al. Emergent ascomycetes in viticulture: an interdisciplinary overview. *Front Plant Sci*. 2019. <https://doi.org/10.3389/fpls.2019.01394/full>.
189. Tyśkiewicz R, Nowak A, Ozimek E, Jaroszuk-Ścisł J. Trichoderma: the current status of its application in agriculture for the biocontrol of fungal phytopathogens and stimulation of plant growth. *Int J Mol Sci*. 2022;23:2329.
190. Vaksmaa A, Guerrero-Cruz S, Ghosh P, Zeghal E, Hernando-Morales V, Niemann H. Role of fungi in bioremediation of emerging pollutants. *Front Mar Sci*. 2023. <https://doi.org/10.3389/fmars.2023.1070905>.
191. Savoie J-M, Mata G. Growing *Agaricus bisporus* as a contribution to sustainable agricultural development. In: Petre M, editor. *Mushroom biotechnology*. San Diego: Academic Press; 2016. p. 69–91.
192. Baktemur G, Kara E, Yazar M, Yilmaz N, Ağçam E, Akyıldız A, et al. Yield, quality and enzyme activity of shiitake mushroom (*Lentinula edodes*) grown on different agricultural wastes. *NOTULAE BOTANICAE HORTI AGROBOTANICI CLUJ-NAPOCA*. 2022 [cited 2024 Jun 18];50. Available from: <https://avesis.cu.edu.tr/yayin/e4443c9a-dfca-4931-ab90-fcd1bbe4b9d5/yield-quality-and-enzyme-activity-of-shiitake-mushroom-lentinula-edodes-grown-on-different-agricultural-wastes>.
193. Ahmad Zakil F, Xuan LH, Zaman N, Alan NI, Salahutheen NAA, Sueb MSM, et al. Growth performance and mineral analysis of *Pleurotus ostreatus* from various agricultural wastes mixed with rubber tree sawdust in Malaysia. *Bioresour Technol Rep*. 2022;17:100873.
194. Yamanaka T, Yamada A, Furukawa H. Advances in the cultivation of the highly-prized ectomycorrhizal mushroom *Tricholoma matsutake*. *Mycoscience*. 2020;61:49–57.
195. Ji W, Zhang N, Su W, Wang X, Liu X, Wang Y, et al. The impact of continuous cultivation of *Ganoderma lucidum* on soil nutrients, enzyme activity, and fruiting body metabolites. *Sci Rep*. 2024;14:10097.
196. Du B, Xu Y, Dong H, Li Y, Wang J. *Phanerochaete chrysosporium* strain B-22, a nematophagous fungus parasitizing *Meloidogyne incognita*. *PLoS ONE*. 2020;15:e0216688.

197. Ullah TS, Firdous SS, Shier WT, Hussain J, Shaheen H, Usman M, et al. Diversity and ethnomycological importance of mushrooms from Western Himalayas, Kashmir. *J Ethnobiol Ethnomed*. 2022;18:32.
198. Buyer JS, Teasdale JR, Roberts DP, Zasada IA, Maul JE. Factors affecting soil microbial community structure in tomato cropping systems. *Soil Biol Biochem*. 2010;42:831–41.
199. Schmidt JE, Kent AD, Brisson VL, Gaudin ACM. Agricultural management and plant selection interactively affect rhizosphere microbial community structure and nitrogen cycling. *Microbiome*. 2019;7:146. <https://doi.org/10.1186/s40168-019-0756-9>.
200. Sun L, Wang S, Narsing Rao MP, Shi Y, Lian Z-H, Jin P-J, et al. The shift of soil microbial community induced by cropping sequence affect soil properties and crop yield. *Front Microbiol*. 2023. <https://doi.org/10.3389/fmicb.2023.1095688/full>.
201. Zhang R, Li Y, Zhao X, Allan Degen A, Lian J, Liu X, et al. Fertilizers have a greater impact on the soil bacterial community than on the fungal community in a sandy farmland ecosystem, Inner Mongolia. *Ecol Indicators*. 2022;140:108972.
202. Srour AY, Ammar HA, Subedi A, Pimentel M, Cook RL, Bond J, et al. Microbial communities associated with long-term tillage and fertility treatments in a corn-soybean cropping system. *Front Microbiol*. 2020;11:1363.
203. Li Z, Kravchenko AN, Cupples A, Guber AK, Kuzyakov Y, Philip Robertson G, et al. Composition and metabolism of microbial communities in soil pores. *Nat Commun*. 2024;15:3578.
204. Vadakattu G, Germida J. Soil aggregation: influence on microbial biomass and implications for biological processes. *Res J Soil Biol*. 2014;80:1–7.
205. Bian H, Li C, Zhu J, Xu L, Li M, Zheng S, et al. Soil moisture affects the rapid response of microbes to labile organic C addition. *Front Ecol Evol*. 2022. <https://doi.org/10.3389/fevo.2022.857185>.
206. Daunoras J, Kačergius A, Gudiukaitė R. Role of soil microbiota enzymes in soil health and activity changes depending on climate change and the type of soil ecosystem. *Biology (Basel)*. 2024;13:85.
207. Thepbandit W, Athinuwat D. Rhizosphere microorganisms supply availability of soil nutrients and induce plant defense. *Microorganisms*. 2024;12:558.
208. Wei X, Xie B, Wan C, Song R, Zhong W, Xin S, et al. Enhancing soil health and plant growth through microbial fertilizers: mechanisms, benefits, and sustainable agricultural practices. *Agronomy*. 2024;14:609.
209. Gunde-Cimerman N, Plemenitaš A, Oren A. Strategies of adaptation of microorganisms of the three domains of life to high salt concentrations. *FEMS Microbiol Rev*. 2018;42:353–75. <https://doi.org/10.1093/femsre/fuy009>.
210. Johan PD, Ahmed OH, Omar L, Hasbullah NA. Phosphorus transformation in soils following co-application of charcoal and wood ash. *Agronomy*. 2021;11:2010.
211. Saadouli I, Mosbah A, Ferjani R, Stathopoulou P, Galiatsatos I, Asimakis E, et al. The impact of the inoculation of phosphate-solubilizing bacteria *Pantoea agglomerans* on phosphorus availability and bacterial community dynamics of a semi-arid soil. *Microorganisms*. 2021;9:1661.
212. Pandey A, Palni L, Mulkalwar P, Mohammad N. Effect of temperature on solubilization of tricalcium phosphate by *Pseudomonas corrugata*. *J Sci Ind Res*. 2002;61:457–60.
213. Yadav H, Gothwal RK, Nigam VK, Sinha-Roy S, Ghosh P. Optimization of culture conditions for phosphate solubilization by a thermo-tolerant phosphate-solubilizing bacterium *Brevibacillus* sp. BISR-HY65 isolated from phosphate mines. *Biocatalysis Agric Biotechnol*. 2013;2:217–25.
214. Mujahid TY, Subhan SA, Wahab A, Masnoon J, Ahmed N, Abbas T. Effects of different physical and chemical parameters on phosphate solubilization activity of plant growth promoting bacteria isolated from indigenous soil. *J Pharm Nutr Sci*. 2015;5:64–70. Available from: <https://setpublisher.com/index.php/jpans/article/view/1875>.
215. Gupta R, Kumari A, Sharma S, Alzahrani OM, Noureldeen A, Darwish H. Identification, characterization and optimization of phosphate solubilizing rhizobacteria (PSRB) from rice rhizosphere. *Saudi J Biol Sci*. 2022;29:35–42.
216. Liu L, Yan R, Zhu L, Yang Y, Gao Z, Yang W, et al. Balanced phosphorus fertilization enhances soil bacterial network complexity to maintain multifunctionality and plant production in dryland agricultural systems. *Agric Ecosyst Environ*. 2023;356:108647.
217. Akbari DL, Golakiya BA, Bhadania RA. Screening and plant growth promoting activity of drought tolerant endophytic bacteria isolated from wild Poaceae. *J Pure Appl Microbiol*. 2015;9:2619–27. Available from: <https://go.gale.com/ps/i.do?p=AONE&sw=w&issn=09737510&v=2.1&it=r&id=GALE%7CA436439663&sid=googleScholar&linkaccess=abs>.
218. Chang C-H, Yang S-S. Thermo-tolerant phosphate-solubilizing microbes for multi-functional biofertilizer preparation. *Bioresour Technol*. 2009;100:1648–58.
219. Yulianti E, Rakhmawati A. Screening and characterization of phosphate solubilizing bacteria from isolate of thermophilic bacteria. *AIP Conf Proc*. 2017;1868:090015. <https://doi.org/10.1063/1.4995207>.
220. Heidari E, Mohammadi K, Pasari B, Rokhzadi A, Sohrabi Y. Combining the phosphate solubilizing microorganisms with biochar types in order to improve safflower yield and soil enzyme activity. *Soil Sci Plant Nutr*. 2020;66:255–67. <https://doi.org/10.1080/00380768.2019.1704180>.
221. Musarrat J, Khan M. Factors affecting phosphate-solubilizing activity of microbes: current status. *Phosphate solubilizing microorganisms: principles and application of microphos technology*. 2014;63–85.
222. Bargaz A, Elhaissofi W, Khourchi S, Benmrid B, Borden KA, Rchiad Z. Benefits of phosphate solubilizing bacteria on belowground crop performance for improved crop acquisition of phosphorus. *Microbiol Res*. 2021;252:126842.
223. Sanchez-Gonzalez ME, Mora-Herrera ME, Wong-Villareal A, De La Portilla-López N, Sanchez-Paz L, Lugo J, et al. Effect of pH and carbon source on phosphate solubilization by bacterial strains in pikovskaya medium. *Microorganisms*. 2023;11:49.
224. Frąc M, Hannula SE, Bełka M, Jędrzycka M. Fungal biodiversity and their role in soil health. *Front Microbiol*. 2018. <https://doi.org/10.3389/fmicb.2018.00707/full>.
225. Emamalipour M, Seidi K, Zununi Vahed S, Jahanban-Esfahlan A, Jaymand M, Majdi H, et al. Horizontal gene transfer: from evolutionary flexibility to disease progression. *Front Cell Dev Biol*. 2020;8:229.
226. Andrews M, De Meyer S, James EK, Stępkowski T, Hodge S, Simon MF, et al. Horizontal transfer of symbiosis genes within and between rhizobial genera: occurrence and importance. *Genes*. 2018;9:321.

227. Faust K, Lahti L, Gonze D, de Vos WM, Raes J. Metagenomics meets time series analysis: unraveling microbial community dynamics. *Curr Opin Microbiol*. 2015;25:56–66.
228. Aguiar-Pulido V, Huang W, Suarez-Ulloa V, Cickovski T, Mathee K, Narasimhan G. Metagenomics, metatranscriptomics, and metabolomics approaches for microbiome analysis. *Evol Bioinform Online*. 2016;12:5–16.
229. Lahlali R, Ibrahim DSS, Belabess Z, Kadir Roni MZ, Radouane N, Vicente CSL, et al. High-throughput molecular technologies for unraveling the mystery of soil microbial community: challenges and future prospects. *Heliyon*. 2021;7:e08142.
230. Hirsch PR, Mauchline TH, Clark IM. Culture-independent molecular techniques for soil microbial ecology. *Soil Biol Biochem*. 2010;42:878–87.
231. Nadarajah K, Abdul Rahman NSN. The microbial connection to sustainable agriculture. *Plants (Basel)*. 2023;12:2307.
232. Chen X, Henriksen TM, Svensson K, Korsaaeth A. Long-term effects of agricultural production systems on structure and function of the soil microbial community. *Appl Soil Ecol*. 2020;147:103387.
233. Rottinghaus AG, Vo S, Moon TS. Computational design of CRISPR guide RNAs to enable strain-specific control of microbial consortia. *Proc Natl Acad Sci U S A*. 2023;120: e2213154120.
234. Jansson JK, McClure R, Egbert RG. Soil microbiome engineering for sustainability in a changing environment. *Nat Biotechnol*. 2023;41:1716–28.
235. Kaul S, Choudhary M, Gupta S, Dhar MK. Engineering host microbiome for crop improvement and sustainable agriculture. *Front Microbiol*. 2021. <https://doi.org/10.3389/fmicb.2021.635917/full>.
236. Thakur N, Nigam M, Mann NA, Gupta S, Hussain CM, Shukla SK, et al. Host-mediated gene engineering and microbiome-based technology optimization for sustainable agriculture and environment. *Funct Integr Genomics*. 2023;23:57. <https://doi.org/10.1007/s10142-023-00982-9>.
237. Ken K, Prosser JI. The bacteria and archaea. *Soil microbiology, ecology and biochemistry*. 2015;41–76.
238. Conrad R. Microbial ecology of methanogens and methanotrophs. *Advances in agronomy*. Academic Press; 2007. p. 1–63.
239. Wu H, Cui H, Fu C, Li R, Qi F, Liu Z, et al. Unveiling the crucial role of soil microorganisms in carbon cycling: a review. *Sci Total Environ*. 2024;909:168627.
240. Papin M, Philippot L, Breuil MC, Bru D, Dreux-Zigha A, Mounier A, et al. Survival of a microbial inoculant in soil after recurrent inoculations. *Sci Rep*. 2024;14:4177.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.