



Soil microbial resources: Unlocking sustainable strategies for crop productivity and soil health

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ABSTRACT

Using efficient rhizospheric microbes as bio-inoculants is a key factor in promoting agricultural sustainability, as these microbes have been shown to enhance plant growth promotion and crop productivity. Soil microbial communities offer numerous benefits to crops, including improved nutrient uptake efficiency, phytohormone production, improved soil structure, nutrient balance, enhanced plant and soil health, protection against soil borne phyto-pathogens and increased plant resilience to abiotic and biotic stresses. These characteristics of rhizospheric microbes have attracted researcher's attention, as using these microbes individually or in consortia has enhanced soil fertility as well as soil health in a eco-friendly manner. Further, the utilization of multi-omics techniques for exploring the hidden potential of beneficial plant growth promoting microbes is one of the novel approaches that can result in the generation of new biological formulations under changing climatic conditions. This review is therefore focused on the diversity of microbes, their contributions for plant growth promotion and yield with advances in techniques for screening and development of efficient bio-inoculant with a special emphasis on promoting sustainable agriculture practices.

1. Introduction

Traditional agricultural practices, which depend heavily on the excessive use of chemical fertilizers and pesticides to increase yields, have caused major issues for agricultural soils, human health and environmental pollution. These include disruptions to micro-ecological environments, reduced diversity of beneficial microbes, and a decline in soil fertility as well as soil health (Gangwar et al., 2017; Santos et al., 2012). To mitigate the adverse impacts of agro-chemicals while meeting the increasing food demands of a growing population, it is crucial to explore sustainable bio-emerging approaches (Singh et al., 2019). Moreover, recent agricultural practices on a global scale are being focused on sustainable environment and economical developments, with the aim of maintaining soil health, crop productivity without causing any negative or harmful impact on the environment (Umesha et al., 2018). In this context, beneficial rhizospheric microflora, including plant growth-promoting bacteria, fungi, and cyanobacteria, have been effectively employed as plant or soil bio-inoculants to boost

crop yields by functioning as bio-inoculants through direct or indirect mechanisms of microbiota. (Glick, 2018).

The inherent fertility of soil depends on the flourishing microbes in the rhizosphere, as they play a direct or indirect role in shaping plant growth, development, soil well-being, and nutrient absorption (Altomare and Tringovska, 2011; Dubey et al., 2019). Using beneficial soil microorganisms, either alone or combined with mineral or organic fertilizers, can enhance crop productivity while preserving environmental health. This is achieved through their symbiotic relationship with plants (Itelima et al., 2018). Bio-inoculants are living preparations containing efficient nitrogen-fixing, phosphate-solubilizing, or plant growth-promoting eco-friendly strains. They are applied to seeds, seedlings, plant roots, or soil to enhance nutrient availability, boost crop productivity through bio-enhancers, mitigate diseases intensity via antagonistic activities and increase soil organic carbon, thereby supporting soil quality and sustainability (Lalitha, 2017; Pal et al., 2015). Bio-inoculants are typically carrier-based, containing beneficial microorganisms in a viable form (Rodrigues and Rodrigues, 2018). Their role

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in various biological activities makes the soil ecosystem dynamic, promoting nutrient cycling and supporting sustainable crop production (Glick, 2014; Hakim et al., 2021). Considering these factors, this manuscript seeks to outline the growth-promoting impacts of beneficial soil microbes, as well as their influence on crop growth and soil fertility, in pursuit of sustainable agriculture.

2. Diversity and mechanism of beneficial rhizospheric microbes

Soil microbes play a crucial role in the soil ecosystem, enhancing soil structure and promoting plant growth through direct or indirect mechanisms (Fig. 1). Assessing the microbes present in the plant rhizosphere, rhizoplane, or within plant tissues (endophytes) for their individual and combined benefits is highly valuable, given the vast microbial diversity in soil (Miransari, 2010; Fiodor et al., 2021). Rhizospheric microfloras play an active role in signaling with various hosts, and these interactions between soil microbes and hosts significantly impact the growth and development of plants (Igiehon and Babalola, 2018). Commonly employed beneficial microbial inoculants comprise nitrogen-fixing bacteria, phosphorus-solubilizing microorganisms, phosphorus-mobilizing agents such as arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPRs), producers and regulators of phytohormones, and inhibitors of pathogenic organisms via antagonistic activities i.e., cell wall degrading enzymes and HCN production (Grobkinsky et al., 2016; Kasim et al., 2016; Miransari, 2011).

2.1. Nitrogen-fixers

Nitrogen-fixing microorganisms have the remarkable ability to convert atmospheric nitrogen (N_2) into organic nitrogenous compounds. This nitrogen fixation process takes place through symbiotic means (*Rhizobium*/*Frankia*), non-symbiotic methods (*Azotobacter*), and associative mechanisms (*Azospirillum*) (Debnath et al., 2019). The ability to fix atmospheric nitrogen has been limited to certain legume plant species and *actinobacteria* referred as the diazotrophs. Biological nitrogen fixation (BNF), carried out by specific soil microbes, is a key part of the nitrogen cycle. This process is driven by the enzyme nitrogenase, which converts gaseous nitrogen (N_2) into ammonia (NH_3) (Ramamany et al.,

2020). Dominant symbiotic nitrogen-fixing genera include *Rhizobium* sp., *Klebsiella pneumoniae*, and *Beijerinckia* sp. (Ahmad and Kibret, 2014; Yoneyama et al., 2019). Introducing biological nitrogen-fixing organisms into crops or fields can enhance plant growth, reduced the phyto-pathogenicity, and maintain optimal nitrogen levels in agricultural soils (Damam et al., 2016).

Rhizobium is the most common symbiotic bio-inoculant, specifically benefiting leguminous crops by forming root nodules. It is highly favored as a bio-inoculant due to its ability to directly enhance nutrient uptake, boost various phyto-hormones production levels, and indirectly reduce the harmful impacts of soil borne phyto-pathogens. (Mabrouk et al., 2018). Leguminous plants form a symbiotic relationship with nitrogen-fixing rhizobia, which involves signal exchange and the release of flavonoids by the plant to stimulate Nod factor synthesis. This symbiosis can be influenced by reactive oxygen species (ROS) and heavy metals, which may accumulate in nodules as a mechanism to reduce their toxic effects on legumes (Stambulska and Baylak, 2020). The specificity of *Rhizobium* species to legume crops arises from the production of Nod factors tailored to specific host plants (Deshmukh and Dev, 2005). This facultative symbiosis between legumes and rhizobia is triggered by nitrogen deficiency in the host plant. Signal molecules exchanged between the partners lead to the formation of root nodules, where rhizobia transform into nitrogen-fixing bacteroids (Maróti and Kondorosi, 2014). In addition to nitrogen-fixing legumes, non-leguminous plants associate with various bacteria strains such as *Achromobacter*, *Alcaligenes*, *Arthrobacter*, *Acetobacter*, *Azomonas*, *Bacillus*, *Beijerinckia*, *Clostridium*, *Enterobacter*, *Erwinia*, *Desulfovibrio*, *Derxia*, *Corynebacterium*, *Campylobacter*, *Herbaspirillum*, *Klebsiella*, *Lignobacter*, *Mycobacterium*, *Rhodospirillum*, *Rhodopseudomonas*, *Xanthobacter*, *Mycobacterium*, and *Methylosinus* (Debnath et al., 2019). Certain strains are also known to nodulate stem which are referred as *Azorhizobium* existing in *Sesbania rostrata*.

Non-symbiotic nitrogen fixation involves free-living soil bacteria that do not depend on direct symbiosis with host plants, as well as associative nitrogen-fixers found in the rhizosphere of grasses and cereals (Roper and Gupta, 2016). *Azotobacter* is a free-living, non-symbiotic nitrogen-fixing bacterium, where the extent of nitrogen fixation depends on the microbe's carbohydrate utilization (Gomare et al.,

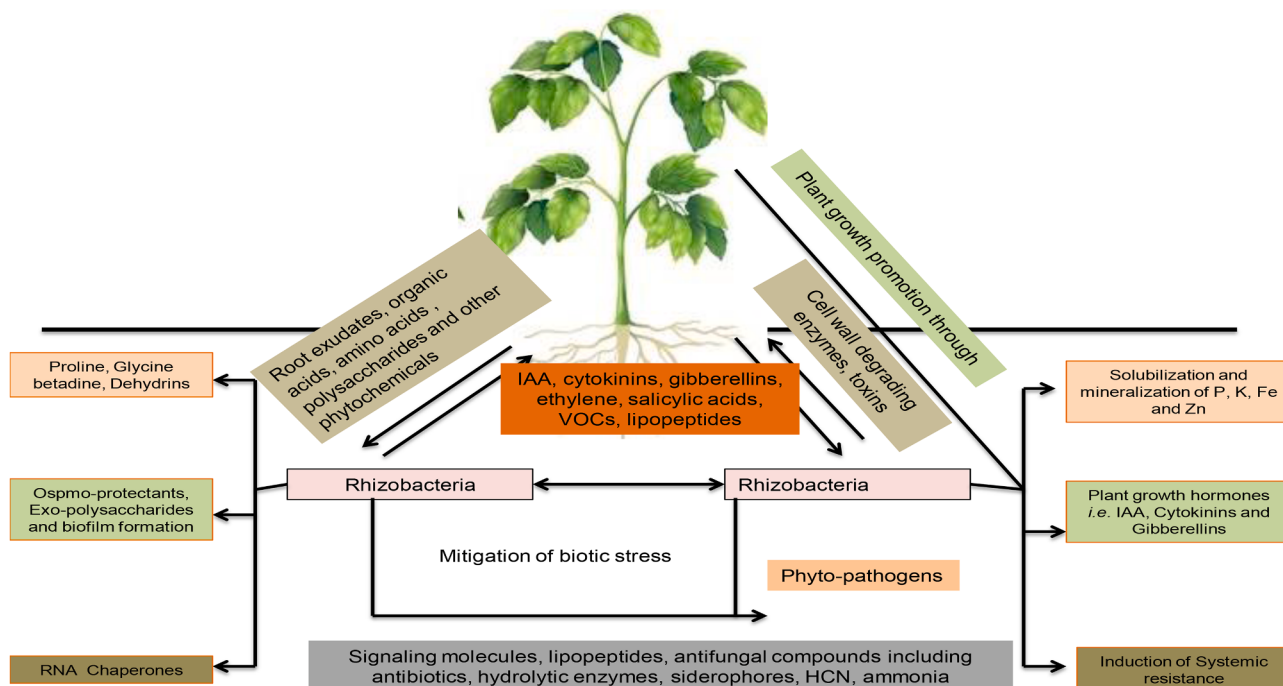


Fig. 1. Schematic representation depicting the probable plant-microbes interactions occurring in the rhizospheric microbiome.

2013). The *Azotobacteriaceae* family consists of two types of bacteria: cyst-forming and non-cyst-forming. *Azotobacter*, a cyst-forming genus, includes six species (*A. chroococcum*, *A. vinelandii*, *A. beijerinckii*, *A. nigricans*, *A. armeniacus*, and *A. paspali*), while *Azomonas*, the non-cyst-forming genus, comprises three species (*A. agilis*, *A. insignis*, and *A. macrocytogenes*) (Singh et al., 2021). The associative nitrogen-fixing bacteria are categorized on the basis of their interactions with plants which can be intercellular endophytic associations or endo-symbiosis (Mus et al., 2016). *Azospirillum*, are the extensively studied gram-negative, facultative, associative N_2 -fixing bacteria inhabiting soil as well as root tissues without nodule formation and are also known for synthesizing various antifungal, antibacterial, and siderophore compounds under deficient conditions (Rana et al., 2023; Steenhoudt and Vanderleyden, 2000). Associative bacteria detect root exudates via chemotaxis and subsequently inhabit the rhizosphere of plants (Santi et al., 2013). The close association of these bacteria with plant roots enables them to acquire essential nutrients such as nitrogen, phosphorus, and other minerals, thereby enhancing the yield of crops like wheat, maize, and rice (Ahmed and Kibret, 2014). Various species of *Azospirillum* have been found in the rhizospheric soil of nearly all major cereal crops and grasses (Altomare and Tringovska, 2011; Raffi and Charyulu, 2021). The endophytic diazotrophs reside and proliferate inside plant tissues without posing any ill-effects. The bacteria, *Azoarcus*, *Herbaspirillum*, and *Gluconacetobacter* are categorized as endophytic diazotrophs owing to their tight colonization with plant tissues (Pedraza, 2008). Numerous species from genera such as *Alcaligenes*, *Azotobacter*, *Burkholderia*, *Clostridium*, *Flavobacterium*, and *Xanthobacter* have been identified in paddy field soil or wetland rice, particularly in the context of endophytic diazotrophs (Rao, 2014).

2.2. Phosphate solubilizers/mobilizers

Phosphorus (P) is one of the major nutrients required in agriculture for the development of crop and various physiological processes (Krishnaraj and Dahale, 2014). The addition of P fertilizers in excessive amount to overcome the unavailability of majority of the plant applied P can lead to serious environmental constraints viz., groundwater contamination and waste water eutrophication (Kang et al., 2011). Plants absorb phosphorus in two soluble forms: mono- and di-basic phosphorus. In contrast, organic forms like inositol phosphate, phosphor-monoesters, phosphor-triesters, and inorganic materials such as apatite are insoluble forms of phosphorus (Mahdi et al., 2012). Micro-organisms with phosphorus-solubilizing abilities can make phosphorus available to plants (Alori et al., 2017). Microbial phosphate solubilization is a well-studied trait, with a focus on bio-inoculant production. In the process of preparing bioinoculant, microorganisms produce organic acids or release protons to attack inorganic P-sources, with chelation, particularly by tri- and di-carboxylic acids like citric and oxalic, enhancing solubilization (Vassileva et al., 2022). Numerous bacterial and fungal species possess the phosphorus solubilization potential and are designated as PSM. The most common soil phosphate solubilizing bacteria includes *Bacillus*, *Pseudomonas*, *Rhizobium*, *Burkholderia*, *Achromobacter*, *Agrobacterium*, *Micrococcus*, *Acetobacter*, *Flavobacterium* and *Erwinia* (Kalayu, 2019). Certain fungi are capable of solubilizing phosphate both in vitro and in soil-plant systems. The success of bio-inoculants can be enhanced by using native or indigenous microorganisms with desirable multifunctional PGP traits, optimized fermentation systems, and nutrient-rich commercial products. When developing bio-inoculants, it is important to consider plant characteristics, soil properties, and microbial profiles (Bouizgarne, 2022; Zhen et al., 2016). The mobilization of soluble phosphorus in soil to plant roots from distant places is facilitated by P-mobilizers. Phosphate solubilizing microorganisms (PSM) can also engage in interactions with arbuscular mycorrhizal fungi in the roots, contributing to the promotion of plant growth through the enhancement of nutrient uptake efficiency (Nacoon et al., 2020). A key example of a phosphorus mobilizer is

mycorrhizal fungi, which form a symbiotic relationship with plant roots (Parween et al., 2017) and have high-affinity mechanisms for phosphorus uptake. In addition to aiding phosphorus absorption, these PSMs also release organic acids, which can alter root structure by increasing total root surface area, volume, the number of root tips, and the extent of root branching, as noted by Fusconi (2013). In essence, the judicious use of suitable PSMs can address plant P demands, enhance P use efficiencies, and support biological nitrogen fixation by diazotrophs, especially in legumes where the N-fixation process has a high P demand (Bargaz et al., 2018; Sulieman and Tran, 2015).

2.3. Plant growth promoting microorganisms (PGPMs)

Microorganisms that promote plant growth are classified into two groups: Plant Growth-Promoting Rhizobacteria (PGPR's) and Plant Growth-Promoting Fungi (PGPF's) (Mishra et al., 2017). Among the many microorganisms found inside (endophytes) or on plants, in soil, and in the rhizosphere, only 1–2 % have plant growth-promoting and crop protection functions (Bakhshandeh et al., 2020). Microbial inoculants benefit plants through three main mechanisms: disease suppression (bio-protectants), improved nutrient uptake (bio-inoculants), and phytohormone production (bio-stimulants) (Sinha et al., 2010). PGPMs support plants by enhancing nutrient availability through biological nitrogen fixation, solubilizing insoluble minerals (such as macro and micro-nutrients), producing phytohormones (like auxins, gibberellins, and cytokinins), sequestering iron by releasing siderophores under iron deficient conditions, and improving stress tolerance via the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Souza et al., 2015; Kalia et al., 2020).

Indirect methods of promoting growth include bio-control against phyto-pathogens through antibiosis or the production of antifungal metabolites, inducing systemic resistance, and generating wall-degrading enzymes like chitinase (Vejan et al., 2016; Kalia et al., 2020). The intensive agricultural management practices and the cultivation of exhaustive crops leading to soil degradation much faster than its replenishment (Rashid et al., 2016; Yang et al., 2020; Pimentel, 2006). In addition, practices such as shortened crop rotations, reduced intercropping, residue burning, and declining ability of soils to retain nutrients, moisture, and structure, as well as maintain a favorable pH (Reytar et al., 2014; Yang et al., 2020), can collectively reduce the soil's ability to support disease-suppressing beneficial microbes, especially rhizospheric micro-flora (Hilton et al., 2021; Peralta et al., 2018). The characteristic PGPR's comprises members of genera, *Mesorhizobium*, *Erwinia*, *Bacillus*, *Burkholderia*, *Azospirillum*, *Flavobacterium*, *Serratia*, *Azotobacter*, *Pseudomonas*, *Agrobacterium*, *Rhizobium*, *Thiobacillus*, *Acinetobacter*, *Frankia*, *Streptomyces*, *Bradyrhizobium*, *Arthrobacter*, *Sphingomonas* (Wani and Gpalkrishana, 2019), whereas the PGPF's includes, *Aspergillus*, *Fusarium*, *Trichoderma*, *Penicillium*, *Piriformospora*, and *Phoma*, which also stimulates numerous plant growth promoting traits in the different cereals and legume crops (Hossain et al., 2017).

2.4. Zinc solubilizers

Zinc (Zn) is the most dominant micro-nutrient required in relatively small concentration in plants (Hafeez et al., 2013). The uptake of zinc in plants occurs in the form of divalent cation, however, soil comprises only a minor fraction of soluble Zn and rest is available in the form of insoluble complexes and minerals (Alloway, 2008). An optimum amount of zinc (Zn) is essential due to its pivotal role in the nutritional and physiological processes of organisms (Hughes and Poole, 1989). Additionally, zinc serves as a metal activator and co-factor for numerous enzymes (Parisi et al., 1969). Fungal or bacterial microbiota, play a crucial role in increasing zinc availability in soil and enhancing zinc uptake by plants through the improvement of solubilization efficiency via microbial interactions. The soil's zinc deficiency can be addressed by introducing Zinc-solubilizing microorganisms. These microbes produce

organic acids that dissolve insoluble zinc compounds such as zinc sulfate, zinc carbonate, and zinc oxide in the soil. Furthermore, they can modify the pH of the soil in the plant's rhizosphere and increase zinc solubility through chelation (Kamran et al., 2017). Alternatively, rhizospheric microbes have the ability to provide crops with mineral nutrients, including zinc, which have low mobility, ensuring that the plant's nutritional demands are met (Mumtaz et al., 2018; Shaikh and Saraf, 2017). Notable zinc-solubilizing fungi (ZSF's) belongs to genera like *Absidia*, *Penicillium*, *Paxillus*, *Hymenoscyphus*, *Oidiodendron*, *Suillus*, *Emericella*, *Beauveria*, and *Trichoderma* (Kushwaha et al., 2020). Similarly, the Zn solubilizing plant growth promoting rhizobacterial strains include *Pseudomonas*, *Rhizobium*, *Bacillus*, *Azospirillum*, *Gluconacetobacter*, *Burkholderia*, *Serratia*, *Acinetobacter* and *Cyanobacteria* have been reported (Mumtaz et al., 2017). Nine out of fifty isolates were found to solubilize Zn, among which *Serratia* sp. was found as the most efficient strain to promote the growth and yield of wheat (Abaid-Ullah et al., 2011). Goteti et al. (2013) reported Zn solubilization in P29, P33, and B40 strains on ZnCO₃ and ZnO incorporated solid medium. Moreover, a noteworthy increase in the total dry biomass and uptake of nitrogen (N), potassium (K), manganese (Mn), and zinc (Zn) was observed in maize when strain P29 was inoculated during seed planting in pot conditions. In a study by Kamran et al. (2017), fourteen and ten zinc-solubilizing isolates were isolated from the rhizosphere of wheat and sugarcane, respectively, and reported beneficial effects on wheat observed under pot conditions.

2.5. Potash solubilizers

Potassium (K) is the third imperative macro-nutrient which is absorbed as cation by plants and performs essential role in various plant processes including photosynthesis, growth, metabolism, assimilation rate and accumulation of sugars (Guo et al., 2019). Potassium plays a vital role in the plant and human health through the microbial interactions. In the crop plants K helps in the activation of various enzymatic metabolic pathways which are involved in the protein synthesis, energy metabolism and transportation of solutes particles through the cytoplasmic membrane. Potassium also very important for inorganic anions transportation and the maintenance of proton gradients in cytoplasmic membrane through pH homeostasis. This macro-nutrient is involved in the stomatal movement, photosynthesis, sugar transportation through phloem. In the human K minerals helps in the secretion of various hormones, regulation of electrical activity in the heart, mineral corticoid action, growth and development of body through the protein and carbohydrate metabolism as well as renal concentration.

The excess usage of potash containing agro-chemicals have in the soil precipitation so the soil microbiologists/ researchers are focussing their efforts on developing bio-emerging alternative and eco-friendly strategies to minimize this K limitations to the crop plants. The Application of K-solubilizing micro-biota as plant bio-inoculants is a sustainable and alternative way to improve a positive impact on the crop production and their quality and also help in the replacement of chemical inputs. KSMs might be considered as the various bio-resources involved in releasing K in soluble form for crop plants via capsule absorption, acid production, complexation and enzymolysis reactions through exo-polysaccharide productions (EPS) (Masood and Bano, 2016). Numerous potassium solubilizing microbes (KSM) have been reported to solubilize K from K-bearing minerals (fixed and insoluble forms) into accessible forms by mechanism of organic acids production (namely oxalic acid, tartaric acids, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, lactic acid, propionic acid, glycolic acid (Etesami et al., 2017; Gundala et al., 2013). The potassium solubilizing bacteria (KSBs) are *Paenibacillus* sp., *Bacillus mucilaginosus*, *Bacillus edaphicus*, *Bacillus circulans*, *Acidithiobacillus ferrooxidans*, *Pseudomonas*, and *Burkholderia* (Meena et al., 2016) and fungi namely *G. intraradices*, *Aspergillus terreus*, *A. niger*, *Glomus mosseae*, and *Penicillium* sp. (Etesami et al., 2017).

Bhattacharya et al. (2016) reported that the *Acinetobacter soli* have

a K solubilizing potential through the organic acids production. Similarly, abiotic stress tolerating KSB including *Acinetobacter calcoaceticus*, *Streptomyces laurentii* and *Penicillium* sp. have been reported (Kour et al., 2020; Yadav, 2022). In a research demonstrated that the co-inoculation of K solubilization (*Bacillus* sp.) and free living N-fixing *Azotobacter* sp. was reported for enhancing the plant growth promotion activities of sudan grass (Basak and Biswas, 2010; Dhamathia et al., 2025). In another study, *Bacillus amyloliquefaciens* was noticed as potential indigenous K solubilizing and it inoculation on the cold stressed wheat was solubilizing and it inoculation on the cold stressed wheat resulted in the alleviation of cold stress (Verma et al., 2015).

In conclusion, the soil microbiologist community is significantly concentrating on more exploration of potential indigenous microbial communities of P solubilizers with additional multifarious PGP traits. Further, understanding the genetic and molecular level study behind the potassium solubilization and mobilization would be more beneficial for agricultural and environmental sustainability under changing climatic conditions.

2.6. Sulphur mobilization

In agricultural soils, sulphur mainly exists as sulfate esters or carbon-bonded sulphur, such as sulphonates or amino acid sulfur, which together account for more than 95 % of the total sulfur content (Kertesz and Mirleau, 2004). Sulphur containing different metabolites have been found to contribute in various physiological and biochemical process such as significant acquisition of essential nutrients, nodule formation and their biomass in the leguminous crops, biological nitrogen fixation by certain diazotrophic microbial diversity, prevention of oxidative damages and protection of crop plants from soil borne phyto-pathogens as well as mitigation of abiotic stresses (Mawad et al., 2021; Zechmann, 2020; Carrion et al., 2018). Interestingly, sulphation of nodulation factors is an essential for making nodules on alfalfa plants by specific *Rhizobium meliloti* strains. Nodulation (Nod) genes i.e., NodH, P and Q are involved in transferring sulphate moiety on the nodulation factor in *R. meliloti*, which confers specific host to synthesized nodules in the alfalfa crop only. These certain nodulation factors are synthesized in the different rhizobial strains, when flavonoid molecules released by specific leguminous roots bind with the NodD protein and cause activation of other nodulation (nod, nol and NOE) genes (Bekele and Yilma, 2021). Within the soil ecosystem, sulfur undergoes a series of interconnected oxidation-reduction reactions involving both inorganic and organic sulphur compounds (Sorokin, 2003).

Microbial desulfurization, driven by a bacterial multi-component mono-oxygenase system, plays a key role in converting organically bound sulfur compounds into inorganic sulfates in the soil (Gahan and Schmalenberger, 2014). Fox et al. (2014) showed that growth promotion of *Lolium perenne* was demonstrated through the role of sulphur-mobilizing bacteria. Moreover, the connection between sulfur assimilation and symbiotic nitrogen fixation was clarified through the disruption of the sulfonate sulfur utilization gene *ssuD* in both *Bradyrhizobium japonicum* (USDA110) and *Sinorhizobium meliloti* (RM1021), resulting in a pronounced nitrogen-deficient phenotype in the host plants (Speck et al., 2019). Gahan et al. (2021) recently studied the role of the arbuscular mycorrhizal symbiotic partnership in promoting organo-sulfur desulfurization by bacteria in the hyphosphere, which is the soil surrounding the fungal hyphae but not directly attached to the roots.

Various researchers reported that the rhizospheric microbial community produce a low molecular weight, volatile organic compounds (VOCs), which inhibiting the growth and metabolic pathway of various phyto-pathogens leading to suppression of the plant diseases (Ossowski et al., 2017). In the addition, microbial VOCs have also been reported to modify the root structure of the crop plants to improve early colonization with a specific microbes (Werner et al., 2016). VOCs released in the rhizosphere have been grouped in various chemical classes such as

sulphides, fatty acid derived molecules, terpenoids, benzenoids, nitriles and various phenolic compounds etc. (Werner et al., 2016). According to Hernandez-leon et al. (2015) demonstrated that S-containing VOCs were most abundants such as sulphide, which contributed to biological control against *Botrytis cinerea* and protected the *Medicago truncatula* plant from *Botrytis cinerea* infection and reduced the stem disease symptoms and root browning.

Similarly, Carrion et al. (2018) also reported that members of Burkholderiaceae family were more abundant in disease suppressive soils and representative strains such as *Burkholderia pyrrocinia*, *Paraburkholderia caledonica*, *P. hospita* etc. inhibited hyphal growth of *R. solani* by 70 % as compared to un-inoculated control. Inoculation with sulphur oxidizing bacteria having additional multifunctional plant growth promoting activities are being advocated worldwide to reduce dependency on agro-chemicals in integrated nutrient management systems (Wang et al., 2022). Therefore, major efforts are being made to characterize and screening indigenous potential beneficial microflora having sulphur oxidizing capacity along with various PGP activities or antagonistic activities from the rhizospheric soil which might be exploration as a low cost input, eco-friendly strategy to improve essential nutrient availability for the growth of crop under sustainable agriculture ecosystem (Manzoor et al., 2021; Kumar et al., 2022b; Chaudhary et al., 2023).

3. Screening of microbial diversity for effective bio-inoculant formulation

The microbial communities possess prodigious agronomic significance attributed to production of plant growth regulators that directly stimulate growth and facilitate plant nutrient uptake. Thus, there is enormous potential of these microbes to be used as bioinoculant agents for various crops in different climatic and geographical habitats (Hafeez et al., 2006). The growth characteristics and optimum growth conditions are the prerequisite factors required for selection of an efficient indigenous microbial strain. Other important factors include the proper

formulation of microbial inoculants, the method of application (Fig. 2), and their shelf life (Itelima et al., 2018). Choosing an effective plant growth-promoting strain is a crucial first step in developing a microbial inoculant. The selected strain must be genetically stable, non-pathogenic, host-specific, and compatible with the natural microbial population (Wani and Gopalkrishnan, 2019).

Majority of the microbial strains fails to perform under field conditions owing to improper formulation involving poor compatibility and carrier stability (Stamenkovic et al., 2018). For an ideal bio-inoculant formulation, the goal is to optimize the chances of inocula survival. This involves creating the most suitable micro-niche for the microbial strain, coupled with protective measures (either physical or chemical) to ensure prolonged viability. This strategy aims to maintain the necessary viability of the inoculant during storage (Flores-Felix et al., 2019). The formulation comprises mixing of microbial inoculant with carrier which can be liquid, powder, granules, and encapsulated cells (Bashan et al., 2014). Solid formulations involve carriers which can be either inorganic or organic and are categorized on the basis of the particle sizes or method of application.

In primary solid formulations, carriers like peat, charcoal, compost, agro-industrial residues, vermiculite, perlite, rock phosphate, calcium sulfate, and polysaccharides are frequently utilized (Sahu and Brahmaprakash, 2016). Conversely, in liquid bio-inoculants, microbial strains are typically modified with water, oil, or polymers. (osmoprotectant, sticking agents, and additives) which enhance viscosity of cell-suspension, stability and capacity of dispersion (Vassilev et al., 2020). The formulation is a multistep process that differs among the type of strain used, soil types, environmental and storage conditions (Herrmann and Lesueur, 2013). In addition to the factors mentioned above, certain soil properties, such as neutral pH, adequate moisture, optimal organic carbon levels, and low salinity are essential for selecting microbial inoculants, as these conditions promote microbial early colonization, various PGP activity, and survival (Thilakarathna and Raizada, 2017). Moreover, when screening inoculants, it is important to note that the soil adaptability range for many microbial inoculants is not

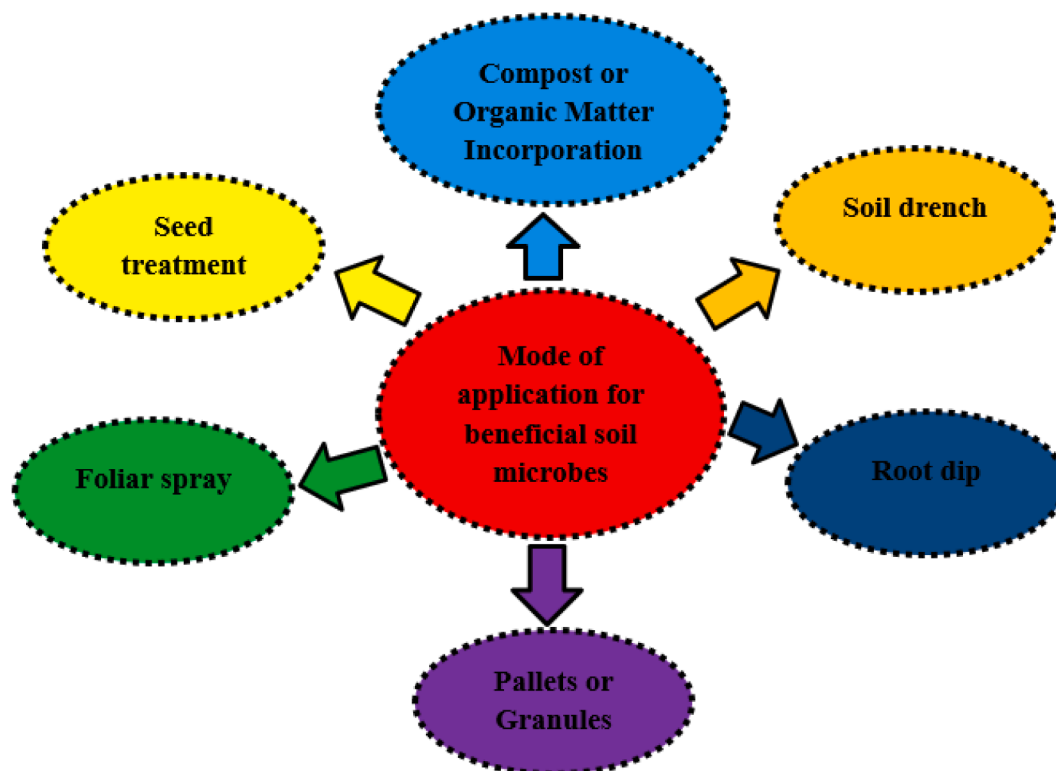


Fig. 2. Mode of application of beneficial soil microbes as bio-inoculants.

well-defined. Therefore, unfavorable soil conditions should be addressed before inoculation, unless the inoculant is designed to tackle a specific soil issue (O'Callaghan et al., 2022). It is widely recognized that soil pH influences microbial community structure and function, as well as the overall microbial biomass in the soil (Fierer, 2017).

4. Applications of beneficial soil microbes

4.1. Improvement of nutrient uptake, growth and crop yield

The application of rhizospheric microbes as bio-inoculant enhances crop yield, plant growth along with increased physio-chemical soil properties (Fig. 3) (Javorekova et al., 2015). While the benefits of bio-inoculants can vary across different crops, all microorganisms generally promote growth through similar mechanisms. These include enhancing nutrient availability, directly influencing plant hormone levels, and indirectly reducing the harmful impacts of phyto-pathogens (Mahanty et al., 2017). There are numerous studies suggesting enhancement in agronomic attributes due to application of bio-inoculants and are summarized in Table 1.

4.2. Enhancement of soil fertility and soil health

Maintaining soil health is essential for long-term productivity, stability, and fertility, which are necessary for plant growth. Soil health includes biological, chemical, and physical properties, with microorganisms playing a key role. Indicators such as microbial diversity, enzyme activity, and soil organic matter content offer reliable ways to assess soil health, providing immediate insights into its current state (Rincon-Florez et al., 2013). Among these indicators, there is an increasing focus on studying rhizospheric microorganisms in their specific environments, recognizing their close relationship with soil structure and function. Furthermore, rhizospheric microorganisms respond quickly to disturbances, as noted by Arias et al. (2005). These

microorganisms have multifunctional enzyme systems that carry out various nutrient transformations, helping to maintain soil balance and health (Ramasamy et al., 2020). The microbiota residing in soil have close associations with their surroundings and act as best indicators of soil health as they quickly react to alterations in soil eco-system attributed to higher surface to volume ratio. Due to involvement of beneficial rhizospheric microbes in numerous soil processes, these microbes can be exploited for the soil health improvement (Saha et al., 2016) (Table 2). Soil enzymes, such as β -glucosidase, cellulase, protease, urease, and phosphatase, play a crucial role in bio-geochemical cycling, especially for carbon, nitrogen, and phosphorus. They reflect the metabolic needs of rhizospheric microorganisms and the availability of essential nutrients, which are essential for breaking down organic matter and using accumulated soil organic matter to release important nutrients (Burns et al., 2013; L. Yang et al., 2018). These enzymes are critical for soil functionality as they significantly contribute to organic matter decomposition, transformation processes, and nutrient cycling (Jesus et al., 2016).

Soil enzyme (biological indicators) activity is closely linked to the metabolic requirements of the soil microbial community and the nutrient pool in the soil. These enzymes are classified into hydrolases and oxidases, which break down substrates and release nutrients into the soil. For example, urease helps microbes acquire nitrogen by catalyzing the breakdown of urea, while β -1, 4-glucosidase, a hydrolytic enzyme produced by microbes, targets polysaccharides. Acidic and alkaline phosphatases are key for phosphorus acquisition (Hai-Ming et al., 2014). In a study by Yu et al. (2016), soil microbial community changes and enzyme activity were analyzed after amending with organic compounds like sorbitol and mannitol. The results showed shifts in both microbial profiles and enzyme activities.

5. Advances in screening of efficient bio-inoculants

The screening of microbial communities by traditional cultivation

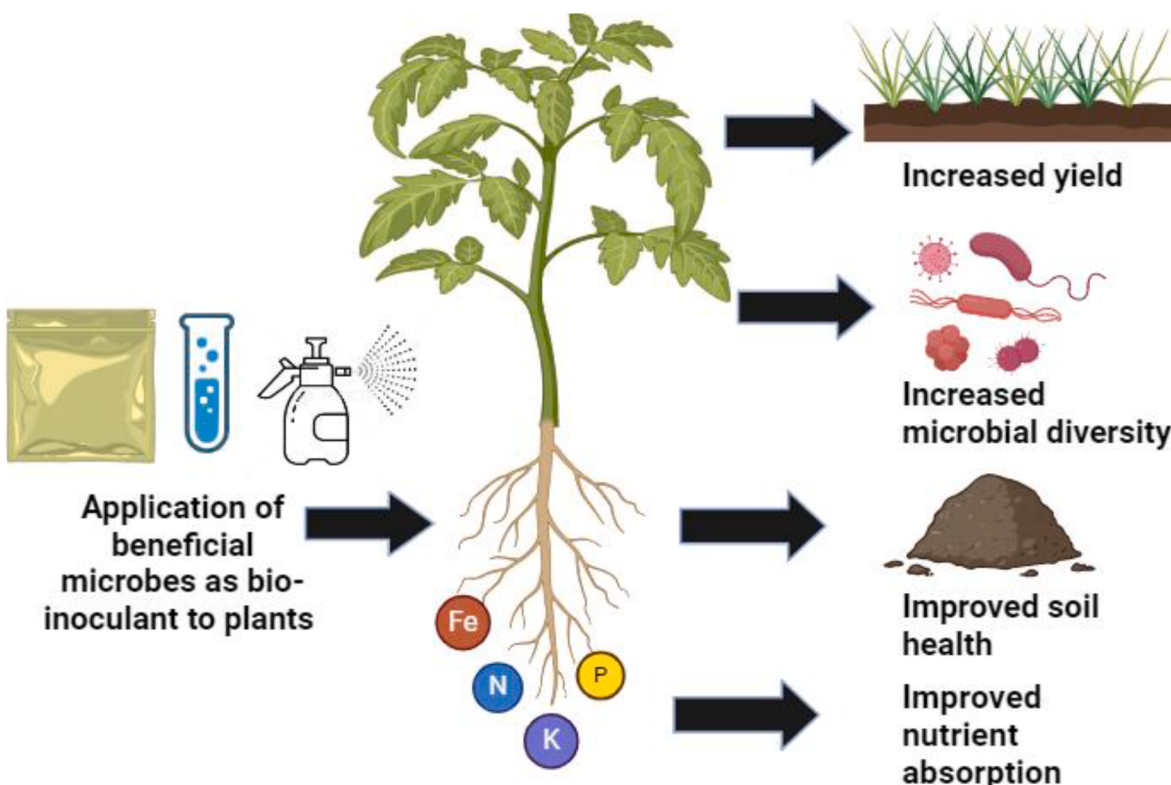


Fig. 3. Beneficial effects of soil microbes as bioinoculants in plant-soil system.

Table 1

Agronomical effects of inoculation with bio-inoculants in different crops.

Crop	Microbial Inoculant	Mode of application	Growth conditions	Crop Response	Reference
Soybean	<i>Bradyrhizobium</i> +PGPR	Seed	Field	Increased nodule number, nodule biomass, root and shoot biomass	Zeffa et al. 2020
Wheat	<i>Azotobacter chroococcum</i> + PGPR	Root Dip	Pot	Increased Shoot height and plant dry mass Enhanced available phosphorus potassium in the soil along with enhanced N, P, and K content of wheat	Wang et al. 2020
Mungbean, Soybean	<i>Bradyrhizobium</i> strains and <i>Streptomyces griseoflavus</i>	Seed	Greenhouse	Increased Shoot growth Enhanced nodulation ability Increased N fixation Increased NPK uptake	Htwe et al. 2019
Maize	Plant growth promoting <i>Streptomyces</i>	Seed	Field	Increased root and stem length and no. of leaves Antagonistic effect against <i>Fusarium</i>	Olanrewaju and Babalola, 2019
Wheat	Plant growth promoting <i>Planomicrobium chinense</i> , <i>Bacillus cereus</i> and <i>Pseudomonas fluorescens</i>	Seed	Field	Significant increase in the chlorophyll, sugar and protein content Significantly enhanced the yield parameters (i.e. plant height, spike length, grain yield and weight) Enhanced accumulation of macronutrients, total NO ₃ -N and P concentration and soil moisture content of rhizosphere soil	Khan et al. 2019
<i>Phaseolus vulgaris</i> L.	<i>Rhizobium</i> and PGPR (<i>Paenibacillus polymyxa</i> and <i>Bacillus megaterium</i>)	Seed	Greenhouse	Higher root and shoot dry weight Enhanced nodulation ability Higher nodule fresh weight	Korir et al. 2017
Wheat	<i>Pseudomonas fragi</i> , <i>Pantoea dispersa</i> , <i>Pantoea agglomerans</i> , <i>E. cloacae</i> and <i>Rhizobium</i> sp. (Zn solubilizing and PGP activities)	Seed	Greenhouse	Higher shoot and root lengths and dry weights Highest zinc content in shoot and root	Kamran et al. 2017
Wheat	PGPR+ Arbuscular mycorrhizal fungi (AMF)	Seed	Field	Enhanced above ground biomass yield and plant N and P concentration	Saia et al. 2015
Lentil	<i>Rhizobium</i> + PGPR	Seed	Axenic	Significantly enhanced seedling germination and vigour, root and shoot length, root and shoot fresh and dry weight	Kaur and Khanna, 2014
Rice	<i>Pseudomonas putida</i> , <i>P. fluorescens</i> and <i>Azospirillum lipoferum</i>	Seedling dip	Field	Increased plant growth, higher chlorophyll content and root and shoot dry mass Higher Iron and zinc content Increased grain yield	Sharma et al. 2014
Rice	<i>Azospirillum</i> , <i>Sphingomonas</i> and <i>Burkholderia</i>	Seed	Field	Increased rice yield compared with 100 % N chemical fertilization	Araújo et al. 2013
Barley	N ₂ -fixing and P-solubilizing bacteria (<i>Bacillus</i> OSU-142, <i>Bacillus</i> M-3, <i>Azospirillum</i> sp. 245, <i>Bacillus megaterium</i> RC07, <i>Paenibacillus polymyxa</i> RC05 and <i>Raoultella terrigena</i>)	Seed	Field	Increased uptake of macro-nutrients (N, P, K, Ca, Mg and S) and micro-nutrients (Fe, Mn, Zn, and Cu) of grain, leaf, and straw part of the barley	Turan and Sahin, 2013
Maize	<i>Azospirillum</i> and <i>Azotobacter</i>	Seed	Field	Increased dry weights of leaf, stem, and grain Enhanced grain weight Significant increase in leaf area index and crop growth index	Gholami et al. 2012
Wheat	<i>Pseudomonas jessenii</i> (R62), <i>Pseudomonas synxantha</i> (R81) and arbuscular mycorrhiza fungi	Seed	Field	Dual inoculation of wheat with PGPR and AMF increased grain yield by 41 % Higher Raw protein and mineral nutrient concentration of wheat grains (phosphorus, potassium, copper, iron, zinc, manganese) Phosphorus use efficiency of wheat grains increased by 95 %	Mader et al. 2011
Field corn	PGPR + arbuscular mycorrhiza fungi (AMF)	Seedling application	Field	Increased plant growth and yield Significantly enhanced Nitrogen content per gram of grain tissues Significantly higher amounts of N, P, and K with inoculants	Adesemoye et al. 2008
Raspberry	<i>Bacillus</i> OSU-142 (N ₂ -fixing bacterium) and <i>Bacillus</i> M3 (N ₂ -fixing and P-solubilizing bacterium)	Root dip	Field	Significantly increased yield, cane length, no. of cluster per cane and no. of berries per cane Significant improvement in N, P, Ca, Mn and Fe contents of raspberry leaves Significantly effected soil total N, available P, K, Ca, Mg, Fe, Mn, Zn contents, pH and increased available P contents in soil	Orhan et al. 2006

methods (plate count and most probable number) possess numerous constraints that resulted in switching to the molecular ([Agrawal et al., 2015](#)) or cultivation-independent approaches, that usually analysis soil microbiota through 16S sequencing, phospholipid fatty acid (PLFA) measurements, metagenomic based approaches and enzyme assays or substrate utilization assays to measure functional activity of microbial communities ([Jacoby et al., 2017](#)). Molecular methods involve directly

extracting nucleic acids from soil samples ([Bulgarelli et al., 2013](#)). Metagenomics, a revolutionary approach for assessing microbial diversity, examines the complete genomes present in a soil sample. This technique eliminates the need to isolate and cultivate individual species ([Mocali and Benedetti, 2010](#)).

Advancements in genomics and metagenomics offer a promising path for understanding the complex diversity and functions of soil

Table 2

Soil health improvement with bio-inoculants in different crops.

Crop	Microbial Inoculant	Mode of application	Growth conditions	Crop Response	Reference
Wheat	<i>Azospirillum</i> spp. + <i>Azoarcus</i> spp. + <i>Azorhizobium</i> spp. and two mycorrhizal fungal-bacterial consortia, viz. <i>Rhizophagus irregularis</i> + <i>Azotobacter vinelandii</i> , and <i>R. irregularis</i> + <i>Bacillus megaterium</i> + <i>Frateruia aurantia</i> , <i>Bacillus</i> sp., <i>Providencia</i> sp. and <i>Brevundimonas</i> sp.	Seed	Field/ Greenhouse	Increased rhizospheric microbial biomass and the activity of enzymes such as β -glucosidase, α -mannosidase, β -mannosidase, and xylosidase Increased FDA hydrolase, dehydrogenase and alkaline phosphatase activity. Enhanced microbial biomass carbon	Cortivo et al. 2020 ; Rana et al. 2012
Eucalyptus	<i>Bacillus megatherian</i> strain Du07 + Biochar (wheat straw)	Soil	Field	Application of PGPR and biochar singly increased the soil urease activity whereas co-application of PGPR+biochar increased soil sucrose activity, electrical conductivity (EC), and TK concentration.	Ren et al. 2020
Alfalfa (<i>Medicago sativa</i>)	PGPR (<i>Paenibacillus mucilaginosus</i> and <i>Rhizobium</i> , <i>Sinorhizobium meliloti</i>)	Seed	Greenhouse	Significant increase in soil microbial biomass, enzymatic activities, total nitrogen, available phosphorus, and soil organic matter contents Slightly increased rhizospheric microbial diversity.	Ju et al. 2019
Pepper (<i>Capsicum annum</i>)	<i>Bacillus amyloliquefaciens</i>	Soil	Greenhouse	Increased population of total culturable and chitinase producing bacteria Enhanced activities of chitinase and dehydrogenase in soil	Jamal et al. 2018
Barley	N ₂ -fixing and P-solubilizing bacteria (<i>Bacillus</i> OSU-142, <i>Bacillus</i> M-3, <i>Azospirillum</i> sp. 245, <i>Bacillus megaterium</i> RC07, <i>Paenibacillus polymyxa</i> RC05 and <i>Raoultella terrigena</i>	Seed	Field	All bacterial inoculations, significantly increased enzyme activities	Turan and Sahin, 2013
Maize	<i>B. aryabhattai</i> , <i>B. subtilis</i> , <i>Bacillus</i> sp. <i>Enterobacter cloacae</i> , <i>Pseudomonas</i> sp. P29, <i>Pseudomonas</i> sp. P33, and <i>Bacillus</i> sp. B40	Seed/soil	Growth chamber/ pot	Enhancement in the root length, root fresh biomass, and root dry biomass as well as zinc uptake efficiency	Mumtaz et al. 2017 ; Omara et al. 2016 ; Goleti et al. 2013
Rice	<i>Acinetobacter</i> sp. and <i>Serratia</i> sp. <i>Sphingomonas</i> sp., <i>Enterobacter</i> sp. <i>Pseudomonas aeruginosa</i> , <i>Ralstonia pickettii</i> , <i>Burkholderia cepacia</i> , <i>Klebsiella pneumonia</i>	Root dip	Greenhouse	Increase in Zn bioavailability in rhizosphere soils and grain yields and Zn densities in grains	Wang et al. 2014 Gontia-Mishra et al. 2017 Othman et al. 2017
Bean	<i>Rhizobium etli</i> , <i>Rhizobium radiobacter</i> and <i>Rhizobium</i> sp.	Seed	Field	Increased straw and grain yield, harvest index, and agronomic fertilizer use efficiency	Yanii et al. 2016
Cowpea, common bean peas, fenugreek	<i>Rhizobium leguminosarum</i> , <i>Rhizobial</i> strain 4.21, 9.17, 11.2 and 14.1	Seed	Field	Increased vegetative growth parameters, shoot minerals, and yield	Arafa et al. 2018
Cauliflower	<i>Azotobacter</i>	Root dip	Field	Increased morphological characters and yield	Subedi et al. 2019
Mulberry	<i>Lactobacillus</i> sp., <i>Bacillus subtilis</i> , <i>Actinomyces</i> sp., <i>Azotobacter</i> sp., <i>Bacillus polymyxa</i> , <i>Pseudomonas fluorescens</i> , and <i>Rhizobium</i>	Soil	Pot	Increased leaf area and weight	Mustaka et al. 2022
Foxtail millet	<i>Azospirillum lipoferum</i> 60 NR-2, 45 L-1, 45 C-1	Soil	Pot	Increased plant height, dry weight of shoot and root. Increased total N content of shoot, root and grain. Increased panicles and the seed weight	Rao and Charyulu 2005

microbes with remarkable detail. The improvement of metagenomic techniques, including DNA probes, polymerase chain reaction (PCR), and next-generation sequencing, has significantly enhanced our ability to monitor microorganisms in their natural environments. Recent progress in developing accurate biomarkers and macromolecular probes has made it easier to quickly and reliably assess soil microbial communities ([Arias et al., 2005](#)). This advancement contributes to a more efficient understanding of the dynamic and complex world of soil microorganisms. Measuring microbial communities can follow either phenotypic or molecular approaches, with the latter gaining prominence due to the challenges in accuracy associated with phenotypic techniques ([Agrawal et al., 2011](#)). Molecular methods have been pursued by soil microbiologists to overcome these limitations. DNA-based methodologies, microscopic examination of labeled microbes colonizing roots, and labeled nutrient substrates are among the molecular approaches deployed for soil health analysis.

These methods, in conjunction with enzymatic and organism-based techniques, supplement conventional physio-chemical analyses, providing a more holistic assessment of soil diversity and composition. Modern molecular techniques have uncovered microbial diversity that

was previously overlooked, largely because many microbes cannot be cultured ([Agrawal et al., 2015](#)). Methods for assessing microbial diversity in soil include both PCR-based and PCR-independent approaches. PCR-independent techniques, such as nucleic acid re-association/hybridization, carbon source utilization profiling (e.g., CLPP/BIOLOG), fatty acid methyl ester (FAME) analysis, and phospholipid fatty acid (PLFA) analysis, are used to study microbial communities. However, these methods have limitations, including a bias towards culturable microbes and a tendency to favor microbes that can use available carbon sources. These techniques mainly reveal metabolic diversity, rather than providing a full picture of microbial diversity ([Fakruddin and Mannan, 2013](#)).

5.1. PCR-based approaches

Genetic fingerprinting techniques, primarily based on PCR amplification, offer valuable insights into the genetic makeup of microbes. To study prokaryotic diversity, identification, and phylogenetic relationships, PCR-based profiling of 16S rDNA is commonly used ([Fig. 4](#)). This process involves extracting DNA from a culture, bioreactor, or

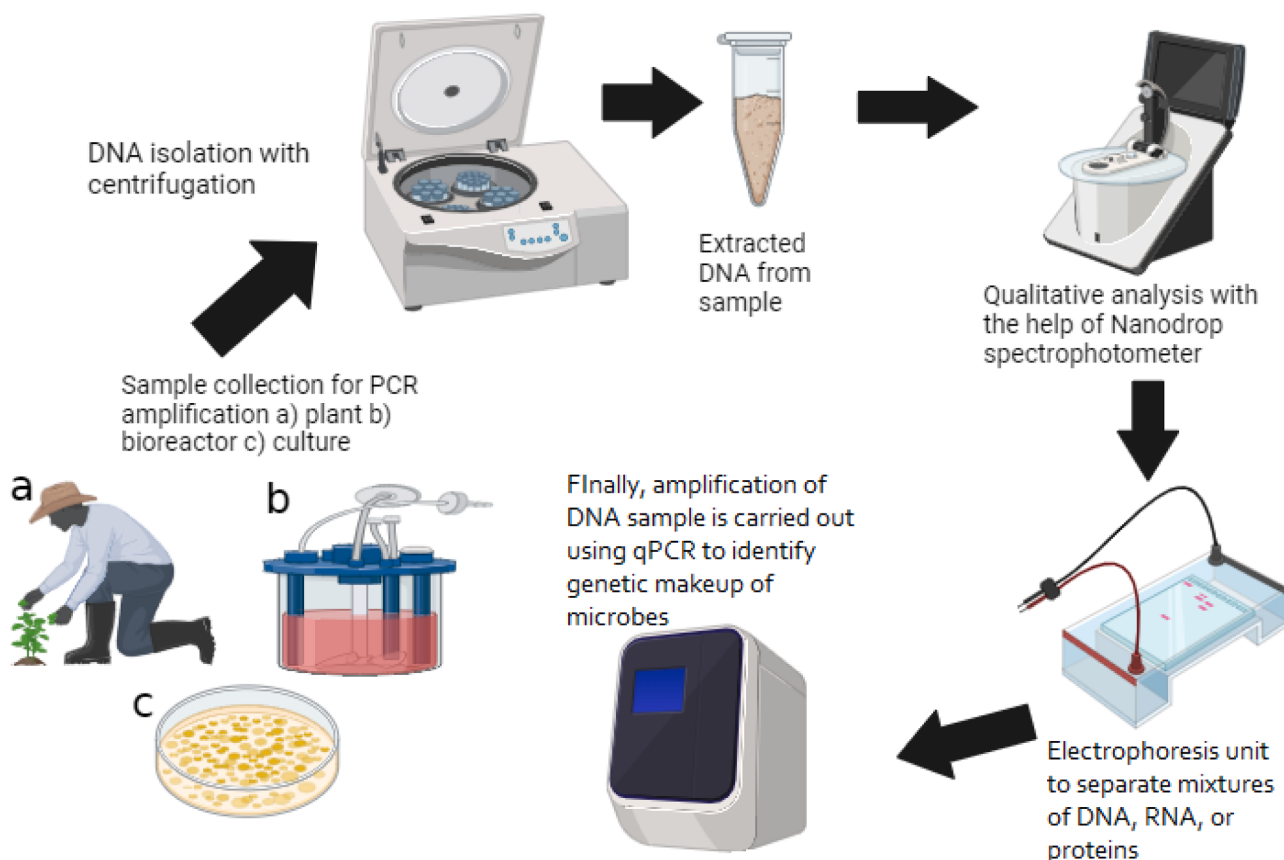


Fig. 4. PCR based approach for molecular characterization of microbes.

environmental sample, followed by amplification of rRNA/rDNA using Polymerase Chain Reaction (PCR) (Sharma and Kaur, 2021). The amplified DNA products are then analyzed, as explained by Ngom and Liu (2014). PCR-based methods are generally divided into two types, based on their electrophoretic migration in agarose or polyacrylamide gels: (1) size-dependent migration, which includes techniques like T-RFLP, ARISA/RISA, RAPD, SSCP, and LH-PCR, and (2) sequence-dependent migration, such as DGGE and TGGE. These techniques allow for the analysis of microbial community structure through the amplified fragments generated by specific primers. PCR techniques based on 16S rDNA, like denaturing gradient gel electrophoresis (DGGE), temperature gradient gel electrophoresis (TGGE), single-strand conformation polymorphisms (SSCPs), amplified ribosomal DNA restriction analysis (ARDRA), terminal restriction fragment length polymorphisms (T-RFLPs), and ribosomal intergenic spacer analysis (RISA), provide a detailed understanding of the community's richness, evenness, and composition (Rawat and Johri, 2014).

Panhwar et al. (2014) used 16S rRNA gene sequencing to identify three potential phosphate-solubilizing bacteria (PSB) strains, which were characterized as *Burkholderia thailandensis*, *Sphingomonas puitosa*, and *Burkholderia seminalis*. In another study, Tahir et al. (2015) assessed the bacterial diversity in the wheat rhizosphere using 454-pyrosequencing of PCR-tagged 16S rRNA gene amplicons. They found that in a wheat-rice system, the dominant bacterial phyla were *Proteobacteria*, *Bacteroidetes*, and *Verrucomicrobia*, while in a wheat-cotton rotation, the most prevalent phyla were *Actinobacteria*, *Firmicutes*, *Chloroflexi*, *Acidobacteria*, *Planctomycetes*, and *Cyanobacteria*. Islam et al. (2016) used 16S rRNA sequencing to characterize ten plant growth-promoting rhizobacteria (PGPR) strains, identifying them as *Pseudomonas stutzeri*, *Bacillus subtilis*, *Stenotrophomonas maltophilia*, and *Bacillus amyloliquefaciens*. Santosa et al. (2018) studied PGPR from the rice field rhizosphere in Indonesia and, using 16S rRNA sequencing, identified

nine strains, including *Pseudomonas aeruginosa* strain RI-98-1, *Stenotrophomonas maltophilia* strain S431, *Bacillus subtilis* strain CEB2, *Bacillus cereus* strain ATCC 14579 clone EA195, and *Serratia nematodiphila* strain HC4. Chen and Liu (2019) analyzed five phosphate-solubilizing bacterial strains isolated from alfalfa rhizosphere using 16S rRNA sequencing, fatty acid composition, and the BIOLOG test. The strains H22, Y11, and Y34 were identified as *Pseudomonas* sp., while Y14 and S32 were identified as *Pantoea* sp. While PCR-based techniques, such as those described above, are useful for identifying the dominant microbes in complex soil environments, they have limitations, including being time-consuming and having relatively low throughput, as noted by Rincon-Florez et al. (2013). To overcome these limitations and streamline the evaluation of soil microbial communities, recent studies have embraced metagenomics combined with bioinformatics. These innovative methods not only provide reliable insights into soil microbial diversity but also offer a more efficient and high-throughput approach, as emphasized by Liu et al. (2006).

5.2. Metagenomic-based approaches

Recently, metagenomics has become a groundbreaking method for studying microbial diversity by analyzing entire genomes within a soil sample (Table 3). This approach eliminates the need to isolate and cultivate individual species, offering a more complete understanding of the microbial community (Mocali and Benedetti, 2010).

The advent of genomics and metagenomics has opened up new ways to explore the hidden diversity of microbes and understand their functions in detail.

Although metagenomics studies provides in-depth understanding of the function of plant microbial communities in the soil, evaluation of the interaction between host plant and beneficial micro-organisms will only be comprehended and studied *insitu* for multifunctional characteristics

Table 3
Beneficial bacterial diversity present in soil and their functions.

Phylum	Function	Reference
<i>Proteobacteria</i>	They are plant growth promoting microorganism and considered as main decomposers in soils, which have substantial role in the decomposition, N fixation, C turnover, degradation of organic matter under diverse substrates.	Berlemont and Martiny, 2013
<i>Actinobacteria</i>	<i>Actinobacteria</i> are recognized as eutrophic denitrifying, being more abundant in nutrients rich environments. They are capable of producing a wide range of C cycling enzymes, and affiliated to aiding in plant residue decomposition, organic matter turnover, humus formation and C sequestration.	Yang et al., 2018 Bao et al., 2021
<i>Chloroflexi</i>	They are oligotrophic and have ability to survive in stressed or nutrient-limited (low C) conditions. Also, they are abundant in the areas of litter decomposition which contribute to the accumulation of halogenated organic compounds in soil.	Chávez-Romero, 2016; Chapman et al., 2017
<i>Planctomycetes</i>	They play a substantial role in global C and N cycles (ammonia oxidation and nitrification-denitrification processes) and anaerobic ammonium oxidation in soil N metabolism	Hu et al., 2020; Li et al., 2012
<i>Firmicutes</i>	They are known as bio-fertilizers and biopesticides and composed of thermophilic, antibiotic and endospore-producing members under harsh conditions. They are considered responsible for the degradation of different C sources, plant polysaccharides, and fix N or denitrify. They also produce β -glucosidase enzyme to break down crop residue.	Battistuzzi and Hedges, 2009; Bukar et al., 2019; Zhu et al., 2016.
<i>Acidobacteria</i>	<i>Acidobacteria</i> belongs to oligotrophic denitrifying micro-organisms, exhibiting high relative abundance in low nutrient environments. The relative abundance of <i>Acidobacteria</i> which are characterized as k-strategists, plays a significant role in the degradation of cellulose, hemicellulose, and lignin.	Pascual et al., 2013.
<i>Bacteroidetes</i>	They are used for accessing sensitivity of agricultural soils and act as biological indicator of agricultural soil usage. Environmental <i>Bacteroidetes</i> are considered to be specialized in the degradation of complex organic matter in the biosphere, especially in the form of polysaccharides and proteins.	Wolińska et al., 2017
<i>Verrucomicrobia</i>	They play a pivotal role in prediction of nutrient status of soil since they are abundant in nutrient deficient soils. Hence, tracking the changes in chemical factors linked to soil fertility under slash-and-burn	Navarrete et al., 2015

Table 3 (continued)

Phylum	Function	Reference
	deforestation and management practices is characterized by <i>Verrucomicrobia</i> .	
<i>Cyanobacteria</i>	They are known to improve soil quality by development of biocrust and improving soil functions. Their application in soil as consortium have known to increase total organic carbon and nitrogen status.	Román et al. 2018
<i>Gemmatimonadota</i>	<i>Gemmatimonadota</i> are found in aquatic environments, such as freshwaters, wastewater treatment plants, biofilms, and sediments. They are suggested to be a keystone group playing an important role in cycling of organic carbon due to their metabolic strategies.	Liu et al. 2020; Mujakić et al. 2022
<i>Nitrospirae</i>	<i>Nitrospirae</i> is a phylum of nitrification bacteria in soils, which plays critical role in both the ammonia-oxidizing and nitrite-oxidizing processes. Hence, it is prevalent in rice-based cropping system.	Huang et al. 2020

or PGP traits. This can be accomplished when metagenomics approaches are combine with other recent emerging techniques such as transcriptomics and proteomics (Trivedi et al., 2021). Advanced sequencing technologies, especially next-generation sequencing (NGS), allow for the direct analysis of microbial DNA extracted from soil (Fig. 5), providing large amounts of data quickly and cost-effectively. NGS has revolutionized our ability to conduct extensive evolutionary and comparative studies that were previously not possible (Weinstock, 2012). Even though, the most commonly used next generation sequencing technique is the Illumina system but recently the soil microbiologist's attentions are shifted towards the application of nanopore and PacBio. The new generation sequencing approaches are that the reads complete genome with 4 to 6 h rather than in days. This technique is very less expensive and does not require any special computer software for the data analysis (Kerkhof et al., 2017). The third generation sequencing technology generate a bacterial and archaeal gene profile from the complete 16S rRNA gene sequencing to provide higher taxonomic relationship at the genus level (Winand et al., 2019).

Metagenomics involves cloning and analyzing microbial DNA directly from environmental samples (Mocali and Benedetti, 2010). By randomly sampling the combined genomes of coexisting microbial communities and sequencing them, metagenomics can offer detailed insights into genetic diversity, species composition, and interactions within natural microbial communities (Fakruddin et al., 2013). Metagenomics can be divided into four sub-categories based on the screening methods used: unselective/untargeted and targeted metagenomics. Unselective metagenomics includes techniques like shotgun analysis and next-generation sequencing, which are chosen for their cost-effectiveness and the simplicity of DNA sequencing. In contrast, targeted metagenomics involves the parallel sequencing of specific target genes, often using ribosomal RNA (rRNA) as an evolutionary clock (Neelakanta and Sultana, 2013; Perito and Cavalieri, 2018).

Sequence-based metagenomics focuses on determining the complete genetic sequence of a sample, which means figuring out the order of all nucleotide bases (A, C, G, and T) in the DNA. This sequence can be analyzed in different ways, such as identifying the full genome of specific organisms within the community or studying the community's genome as a whole. This approach provides valuable insights into evolution and population ecology (Brumfield et al., 2020). In contrast,

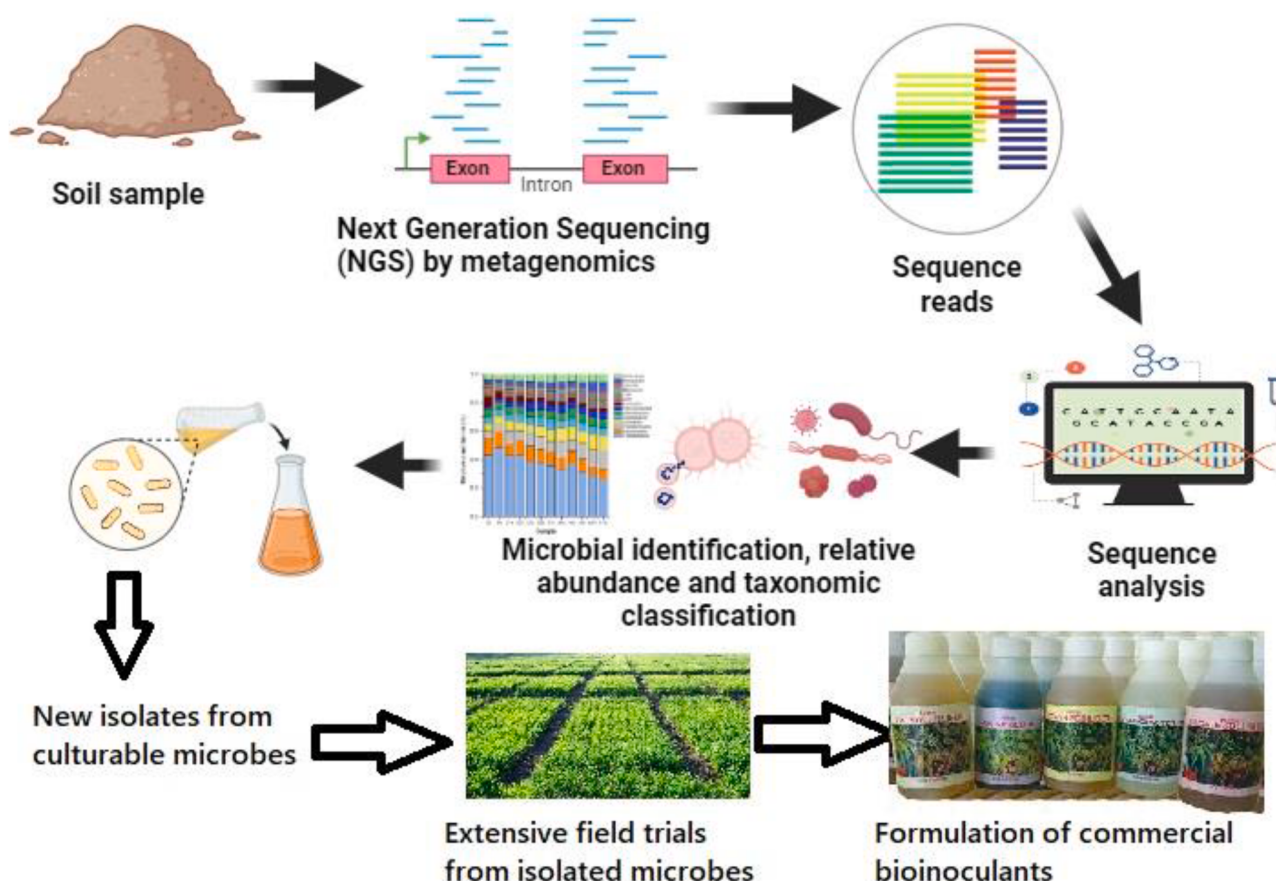


Fig. 5. Metagenomic-based approaches for classification, identification and formulation of bio-inoculants.

function-based metagenomics involves screening metagenomic libraries to discover specific functions or products, like vitamins or antibiotics, produced by microbes in a community. This method helps uncover previously unknown functions in microbes. Recent advancements in function-based metagenomics now allow researchers to directly extract new proteins from microbial communities and identify their metabolites involved in cellular processes (Kunin et al., 2008). The TerraGenome project, a global collaborative effort, was launched to sequence and interpret the soil metagenome, bringing together expertise from the international scientific community (Vogel et al., 2009). The goal of this consortium was to fully sequence a reference soil metagenome (Fuji et al., 2009).

Currently, many molecular information arising from transcriptomics and proteomics strategies are important for the better comprehension of gene content, specific functions and metabolic networks that are translated crop breeding, diseases resistance gene and soil health as well as crop productivity (Pinu et al., 2017). Early transcriptomics studies were performed with the aim of quantification of target microbial strains or gene of interest and rapid detection through real time PCR (RT-qPCR). With this strategies, selection of gene of interest to monitor their expression regulation are commonly made of in-vitro PGP traits through genome mining analysis (Rodriguez et al., 2025). This technique has been very useful in monitoring the expression and regulation of genes with multifunctional PGP traits such as indole acetic acid production (*ipdc*), phosphorous solubilization (*pqq*, *pho A*), antagonistic activities involved in phytopathogens inhibition such as phenazine (*phzF*) and pyrrolnitrin (*prn D*), biological nitrogen fixation (*nifH*) and induced systemic resistance (ISR) via pathogenesis related gene (*PR-1-2*) as well as plant defensive chitinase (*Chit-1*) etc. (Sigh et al. 2020; R. Liu et al., 2020; Imperiali et al., 2017; El-Maraghy et al., 2020). In RNA sequencing approaches have become the standard technique to explore

transcriptomic responses of interaction of PGPRs and host crop plant, providing valuable insights into the gene regulation profiling that promote plant growth in unbiased, genome wide view of gene expression. Recently in the study transcriptomics analysis has reported that co-inoculation with slat tolerating bacterial diversity, significantly influence wheat gene expression involved in different physiological metabolic pathway and stress tolerance mechanisms, with effect more prominent in leaves as compared to roots (Ji et al., 2023).

Ismail et al. (2012) used next-generation sequencing to explore microbial diversity in tropical mangrove soil, discovering a higher diversity of microbes from both bacteria and archaea genera. In a similar study, Ahmed et al. (2018) analyzed microbial diversity in two saline rhizosphere soil samples using a metagenomic approach. They constructed 16S rDNA libraries with bacteria-specific primers through PCR amplification, and a functional metagenome analysis of these libraries revealed a wide variety of phosphatase genes. In another study, Molina-Montenegro et al. (2018) applied shotgun metagenomic technology to compare rhizospheric microbiomes, finding that bacterial species dominated (98 %), followed by eukaryotes (1.77 %) and archaea (0.22 %). The primary genera observed in the rhizospheric soil included *Proteobacteria*, *Actinobacteria*, *Bacteroidetes*, *Acidobacteria*, and *Firmicutes*. Meanwhile, Hara et al. (2019) utilized omics approaches to identify functional N₂-fixing bacteria associated with sorghum. The study involved the examination of bacterial cells extracted from the roots through metagenomic and proteomic analyses, with a majority of the sequences assigned to *nifHDK* of *Bradyrhizobium* species.

Multomics techniques enable the study of the complex interactions between bio-inoculants, plant and phytopathogens. From analysis of genomics, metabolomics/proteomics and transcriptomics profiling of diverse microbial communities, microbiologist can identify potential plant growth promoting traits or the effective combinations for specific

crops and climate conditions. The integration of multiple omics should significant focus on unexploring the functional mechanisms behind crucial soil processes and nutrient cycling which are vital for the provision of ecosystem services and for introducing innovative metrics to assess soil health under intensive cropping systems (Brown et al. 2024; Clagnan et al., 2024).

6. Advances in bio-formulations

The formulation is the important step for successful development of bio-inoculant as the major problem in bioinoculant development is maintaining required microbial population along with its metabolic activity that usually declines after its application in the soil (Fig. 6) (Sahu and Brahmprakash, 2016). Thus, apart from solid and liquid based inoculants, significant advancement in bio-formulation has been achieved in recent years comprising polymer-entrapped inoculant formulations and bio-immobilization which are considered as promising new techniques in agriculture (Herrmann and Lesueur, 2013; Vassilev et al., 2020).

Bio-immobilization technology entails affixing microbial cells to water-soluble polymeric materials such as gellan gum, agar, methoxy-pectin, and many others. The most widely used microbial formulations are alginate and carrageenan (Maćik et al., 2020). The beneficial microbes are immobilized by surface adsorption, flocculation, covalent binding with carriers, cells cross-linking and encapsulation in polymer (Abdelmajeed et al., 2012). In polymer-entrapment, firstly the microbial cells are mass multiplied and then entrapped in suitable polymeric materials which results in formation of beads with living cells inside. The beads are generally degraded by soil microbes and the entrapped cells are released in soil (Deaker et al., 2004; Sahu and Brahmprakash,

2016). The encapsulation of microbial inoculants is more beneficial than free cell formulations as it increases the viability by rendering protection against adverse environmental conditions and reduces the chances of contamination during storage (Schoebitz et al., 2013). The increased viability is directly related with longer shelf life (Mortazavian et al., 2007). The production and application of immobilized-cell formulations prepared from beneficial microbes on large scale in field are still limited due to higher production cost (Bashan et al., 2016).

In agriculture, nano-fertilizers are advanced formulations designed to enhance nutrient uptake efficiency by delivering nutrients in nano-scale particles (1–100 nm). Their exceptionally high surface area improves nutrient absorption and minimizes losses compared to conventional fertilizers (Marchiol et al., 2022). By ensuring precise and efficient nutrient delivery, nano-fertilizers optimize plant growth, reduce the need for excessive chemical fertilizer use, and lower environmental impacts (Qureshi et al., 2018). The nanoscale size allows targeted nutrient release directly to plants, reducing soil contamination and leaching into water reservoirs (Guo et al., 2018). Controlled nutrient delivery prevents over-fertilization, thereby minimizing soil and water pollution while simultaneously improving crop yield and plant resilience. The adoption of nano-fertilizers supports sustainable farming by reducing agricultural pollutants, conserving resources, and fostering healthier ecosystems (Jakhar et al., 2022; Mim et al., 2025). Overall, their application offers multiple advantages, including better nutrient management, increased productivity, long-term sustainability, and cost-effectiveness-making nano-fertilizers a promising innovation for modern, eco-friendly agriculture (Kalia et al., 2019).

The advanced technologies which employ polymeric nanoparticles or nano-formulations or nanoparticle coatings provide new insights for the development of bio-formulations (Daniel et al., 2019; Vassilev et al.,

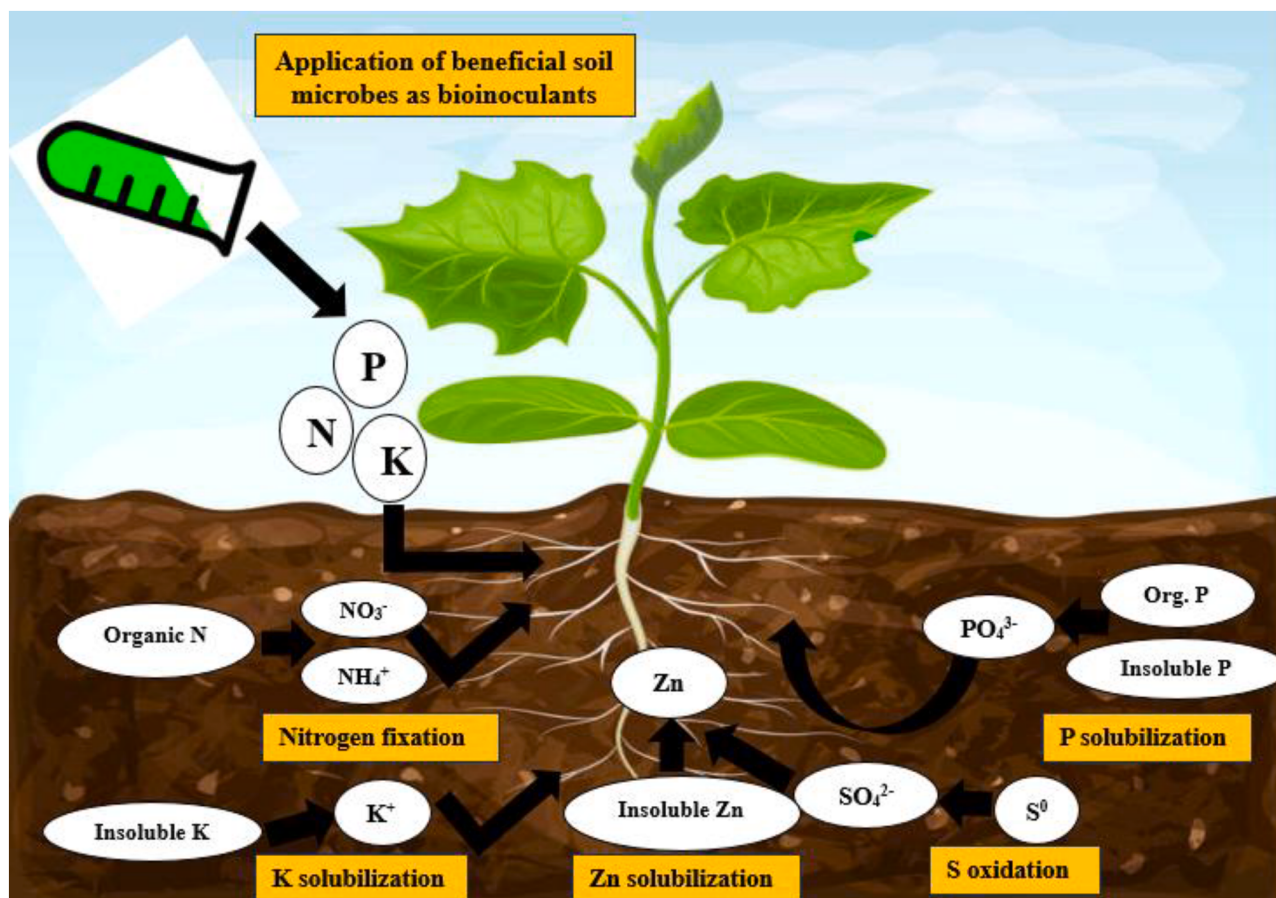


Fig. 6. Application and mechanism of beneficial soil microbes as bioinoculants.

2020; Bailey et al., 2010). Nanotechnology has the ability to revolutionize the conventional agriculture sectors by using novel innovative approaches for absorption of essential nutrients, precision farming, induce disease tolerance and its treatment or control measures (Prasad et al., 2017; Zafar et al., 2024). The remarkable usage efficiency, absorption rate and minimal nutrient loss of nano-biofertilizers might facilitate efficient nutrient uptake and assimilation in crop plants (Sharma et al. 2023). In addition to applications, this novel emerging idea of nano-mediated precision agriculture would reinforce the requirement for crop production, bio-resource preservation and biogeochemical cycling. By providing early and timely warning of pathogen outbreak, nanosensors have improved crop diagnostic methods (Kashyap et al., 2019). Additionally biosensors are employed to quantitatively determine the presence of toxic and illegal ingredients in agro-chemicals, such as carbamate and organophosphorous compounds (Kumar and Prasad, 2021). Similarly, photosynthetic microalgae-derived NBFs are sensitive to changes in the environment and can detect the presence of toxicants, they can be used as biosensors to identify harmful substances such as insecticides, fungicides, herbicides, heavy metal and various organic volatile compounds (VOCs) in the 1–10 ppb ranges (Tripathi et al., 2022).

7. Constraints in applying soil microbes as bio-inoculants

Constraints in the application of soil microbes as plant nutrition are multifaceted and encompass various challenges that hinder their efficacy and practical implementation in agricultural systems (Fig. 7) (Timmusk et al., 2017). One significant constraint is the variability in microbial performance under different environmental conditions, including soil type, climate, and agricultural practices (Yang et al., 2023). This variability can result in inconsistent outcomes and limit the widespread adoption of bioinoculants. Some soil microbes exhibit host-specific associations with particular plant species or genotypes, limiting their utility across different cropping systems (Jacoby et al., 2017). Inoculant strains optimized for one plant species may exhibit reduced efficacy or compatibility when applied to alternative hosts, thereby restricting their broader applicability in agricultural contexts.

Furthermore, challenges related to the formulation, stability, and shelf-life of microbial inoculants pose hurdles in their production and distribution (Berninger et al., 2018). Factors such as the viability and stability of applied microbes under environmental stresses (Bashan et al., 2014), compatibility with diverse soil conditions (Yang et al., 2023), competitive interactions with native microbiota (Mendes et al., 2013), and nutrient limitations (Glick, 2020) can impede their colonization, survival, and functional activity in the rhizosphere. In addition, challenges such as inefficient delivery systems (Bashan et al., 2016), potential interactions with agrochemicals (O'Callaghan et al., 2022), regulatory obstacles (Deaker et al., 2004), and economic factors (Koskey et al., 2021) hinder the widespread use of microbial-based fertilization methods. Farmers need to be made aware of the negative effects of chemical fertilizer as well as how nano biofertilizer will be more affordable and have longer-lasting effects (Zafar et al. 2024). Overcoming these challenges will require focused research to improve microbial formulations, delivery systems, and management techniques, making them more practical and economically viable for sustainable agriculture.

8. Future perspectives

- While the application of proficient soil microbes as bio-inoculants holds promise for enhancing agricultural sustainability, it's essential to ensure rigorous testing and validation of these microbes in different environmental conditions and cropping systems.
- Standardized protocols must be developed to assess the efficacy, safety, and compatibility of bio-inoculants with existing agricultural practices. This will help ensure reliable results and encourage broader adoption.
- The integration of omics technologies, such as metagenomics, metatranscriptomics, and metabolomics, holds significant potential for unraveling the complex interactions within soil microbial communities and identifying novel microbial candidates with specific functions beneficial for plant growth and soil health. Leveraging these techniques could lead to the development of customized bio-

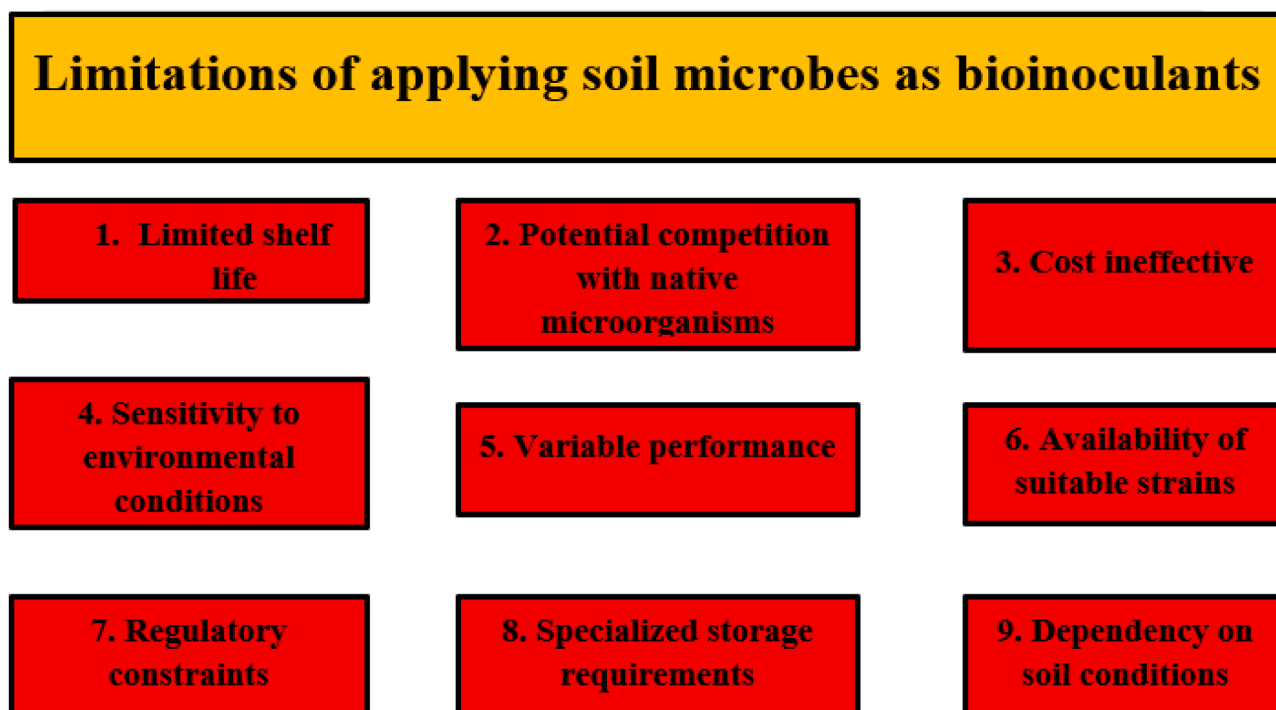


Fig. 7. Limitations of beneficial soil microbes as bioinoculants.

inoculants tailored to suit diverse agroecosystems, thereby optimizing crop productivity while minimizing environmental impact.

- Studying the synergistic interactions between different microbial species can help create highly effective bio-inoculant mixtures. By understanding how specific microbial combinations work together to support each other's functions, we can boost plant growth and improve resilience to various stresses, ultimately supporting sustainable agricultural practices.
- Future research could focus on isolating and characterizing soil microbes that play key roles in improving nutrient use efficiency in plants. By promoting better absorption and utilization of essential nutrients, these microbes can help reduce the reliance on synthetic fertilizers, thus mitigating nutrient runoff and associated environmental degradation.
- Exploiting the remediation capabilities of certain soil microbes can offer dual benefits by improving soil quality while also cleaning up contaminated environments. Investigating the ability of specific microbial strains to degrade pollutants and restore soil health can open up new avenues for sustainable land management and rehabilitation of degraded ecosystems.
- Addressing the practical challenges associated with large-scale production and application of bio-inoculants is crucial for their widespread adoption. Future research could focus on optimizing production methods, developing effective delivery mechanisms, and assessing the economic feasibility of incorporating bio-inoculants into mainstream agricultural practices. This would facilitate the transition towards more sustainable and resilient agricultural systems on a global scale.
- Research should focus on identifying soil microbes that can boost carbon sequestration in agricultural soils. These microbes can help reduce carbon dioxide emissions and promote the formation of stable organic matter through processes like increased root exudation and improved soil aggregation. This not only aids in mitigating climate change but also enhances soil fertility.
- Presently the price/ cost of bioinoculants is also on a higher side, so further one principal aim should also be to cut the high price so that they are accessible to small scale farmers too. Breakthrough technological interventions can make it possible.
- Currently our laboratory research was unable to completely support the implementation of the nano-biofertilizer application strategy within the field of agriculture. To accurately represent the environmental impacts of nanoparticles, an exploratory approach must be implemented in a natural farming or natural environment. In order to evaluate legal and safety concern limitation of nanoparticle dose, government and scientific-based safety requirements should be conducted. Additionally, it is necessary to assess and establish the management of the drawbacks of the used waste materials using genuine natural field application.

9. Conclusion

Soil microbial communities play a crucial role in nutrient cycling, carbon mineralization, and stabilization. While bio-inoculants offer agronomic benefits and increased crop yields, their commercial application is limited due to inconsistent performance under field conditions compared to laboratory results. To improve the use of bio-inoculants, advanced screening techniques, such as PCR-based methods, next-generation sequencing, and metagenomics, are needed, along with efficient growth, storage, shipping, formulation, and application methods. Traditional plate count techniques, which are limited in scope, have given way to molecular methods for exploring microbial diversity. Taxonomists have developed various molecular techniques that allow for the rapid analysis of specific traits within microbial communities. The advent of sequencing tools has introduced a more innovative and efficient approach called integrated omic methods, which include metagenomics, transcriptomics, metaproteomics, and metabolomics.

Metagenomics, for example, involves directly analyzing DNA from environmental samples, bypassing the need for microbial isolation and cultivation. However, no single technique can comprehensively capture the entire range of beneficial microbial diversity. Each method has its own biases at different stages of treatment, with both advantages and drawbacks. The key to utilizing multi-functional beneficial microbes lies in understanding their role as part of a community. While many studies have looked at the impact of inoculating beneficial microbes on crop yields and soil health, there is still a significant research gap when it comes to studying the interactions among multi-functional microbes, plant genotypes, soil conditions, rhizo-microbiome dynamics, and metagenomic approaches. More exploration regarding understanding the mechanism by which nano biofertilizers promote agricultural development is imperative. Since the development of sustainable agriculture using nanotechnology has a very promising future, it may prove to be both an economical and environmentally good strategy. This gap highlights the need for more in-depth exploration of the agricultural potential of these beneficial bio-inoculants.

Declaration of competing interest

None.

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Data availability

No data was used for the research described in the article.

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