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Agriculturally important groups of microorganisms – microbial enhancement of nutrient availability

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Abstract. The increased dependence of modern agriculture on excessive use of agrochemicals and mineral fertilizers, combined with the effects of climate change, will contribute significantly to environmental degradation and loss of soil quality. Consequently, current trends are based on the search for sustainable agricultural practices, in line with the pro-environmental elements of European policy, to reduce energy use and environmental problems, and to provide an adequate supply of high quality, healthy food for an ever growing world population. The production of healthy food is entirely dependent on the availability of nutrients, so the use of biofertilizers with microorganisms is one of the best ways to supplement and increase the availability of nutrients necessary for proper plant growth and yield. Microorganisms are a powerful tool that can provide significant benefits to crops for sustainable agriculture. The aim of this paper is therefore to review the literature on some of the most important groups of microorganisms that are components of biofertilisers. These are those that increase nutrient availability: atmospheric nitrogen-fixing microorganisms, phosphorus-solubilising microorganisms and potassium-solubilising microorganisms. This review therefore distinguishes between different groups of microorganisms and their plant growth promoting mechanisms by which they exert their yield enhancing function to meet the demand for healthy food. Microorganisms that are involved in balanced nutrient cycling and have other plant growth promoting properties (PGP) are an effective way to reduce the use of mineral fertilizers, enabling efficient and sustainable agriculture that maintains a healthy soil for future generations.

Keywords: biofertilizers, sustainable agriculture, plant growth promotion, microorganisms, increased nutrient availability

INTRODUCTION

The rapid growth of the human population has led to global concerns about food security and increased demand for food, particularly crops. There are already around 8 billion people in the world. This number is expected to rise to almost 10 billion in the next 50 years. The issue of global food security is therefore a major challenge for society and the agricultural sector in order to achieve sustainable development, i.e. the eradication of hunger. This challenge has been exacerbated by the ever-increasing demand for food and the fact that arable land is a finite resource. Between 1961 and 2016, global arable land per capita declined steadily from around 0.45 hectares per capita to 0.21 hectares per capita (FAO, 2020). As a result, improving and sustaining crop yields without negatively impacting the environment is a key objective in meeting the world's food and nutritional needs.

All living organisms, including plants, require food for growth and development. In agriculture, the main determinants of plant growth are minerals. In addition to oxygen, carbon dioxide and water, plants require nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), sulphur (S) and magnesium (Mg) in large amounts, while chlorine (Cl), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), nickel (Ni) and molybdenum (Mo) are required in smaller amounts (Kirkby, 2012; Aibara, Miwa, 2014). The solubility of minerals depends on their chemical form, which is influenced by various environmental factors such as water content, pH, redox potential, abundance of organic matter and microorganisms in soils (Kirkby, 2012). Each plant species has an optimal range of nutrient requirements. Below this level, plants begin to show symptoms of nutrient deficiency. However, excessive nutrient uptake can lead to poor growth due to toxicity. Therefore, the correct amount and application of nutrients is important (Uchida, 2000). For example, excessive nitrogen fertilization can cause irregular flowering and delay the harvest date of crops. Excess nitrogen makes plants more susceptible to attack by fungal pathogens. Harmful nitrates accumulate in the tissues of root and leaf vegetables, and cause also desiccation of shoot tips and young leaves, which in turn reduces plant yield (Grzyb et al., 2021).

The essential nutrients provided either by soil minerals and organic matter or by organic or inorganic fertilizers. Recently, inorganic fertilizers have become a topic of interest for many scientists and the public. Due to the growing population, there has been increasing pressure to use agricultural inputs to maintain adequate levels and quality of food produced. Agriculture has long relied on the large-scale use of chemical fertilizers, which are sources of nutrients for plants and thus responsible for increasing crop yields (Krasilnikov, Taboada, 2022). According to the Organization for Economic Co-operation and Development (OECD), chemical fertilizers are defined as substances containing chemical elements that improve plant growth and soil fertility. In inorganic or mineral fertilizers, the nutrients are inorganic salts obtained by extraction and/or physical and chemical processes (OECD, 2008).

Literature data suggest that the use of fertilizers has been responsible for at least a 50% increase in crop yields in the 20^{th} century. Furthermore, it is estimated that without the use of nitrogen fertilizer, average maize yields would decrease by 40% and wheat yields would decrease by 40–57% (Yousaf et al., 2017). FAOSTAT data show that global consumption of the three main fertilizer nutrients, nitrogen (N), phosphate (P_2O_5) and potassium (K_2O), will increase by 7.1% in 2020 compared to 2015 (FAOSTAT, 2024).

Agricultural intensification degrades soil quality and its negative effects have increased in recent decades. This is why current EU environmental policies, including the Green Deal and the EU Biodiversity Strategy, call for the promotion of sustainable agriculture, the reduction of agrochemical use and the protection of biodiversity. However, the use of mineral fertilizers and other agrochemicals has raised many public concerns about the sustainability, safety and security of the food supply. Yet they remain key tools for global food security. With global goals for sustainable agriculture, the problematic effects of mineral fertilizers cannot be ignored. The effects of over-fertilization on the soil environment are briefly described below. Overall, the use of chemical fertilizers is responsible for the decline in soil organic matter (SOM) and humus. Constant use of chemical fertilizers can lead to soil compaction, acidification, soil crusting and soil contamination. In addition, the use of fertilizers affects soil biodiversity and its microbial activity (Pahalvi et al., 2021).

In particular, the rhizosphere microbiota is highly sensitive to anthropogenic changes, including long-term fertilizer inputs (Ai et al., 2013). Soil microorganisms are an important component of the agroecosystem environment due to their annotation in maintaining the function and long-term sustainability of soil ecosystems (Gu et al., 2021). Previous studies have shown that excessive N fertilizations generally alters the diversity, structure and activity of microorganisms in bulk and rhizosphere soil (Sun et al., 2019; Wang et al., 2018; Wei et al., 2018; Chen et al., 2014). Gu et al. (2021) evaluated the response of soil microorganisms to different N application rates in sugarcane soils. The results showed that excessive use of nitrogen fertilizer resulted in a relatively significant increase in the relative abundance of the phyla Proteobacteria, Acidobacteria and Bacteroidetes, and the genera *Sphingomonas* and *Gemmatimonas*. Furthermore, based on the Chao1 and ACE indices, they reported that excessive N fertilizations reduced bacterial species richness, which may be due to the selective pressure of high concentrations of available N and soil pH changes on microorganisms. Fierer et al. (2012) also found that improved soil N availability increased the abundance of copiotrophic bacterial taxa, including Proteobacteria and Bacteroidetes. The aim of the Sun et al. (2019) study was to assess the bacterial and archaeal community structure after 34 years of N fertilizations treatments in *Zea mays* monoculture. Using analysis of the V4 region of the 16S rRNA gene via Illumina technology and bioinformatics processing, the researchers showed that high nitrogen concentrations reduced the diversity of soil bacterial and archaeal communities and changed the relative abundance of dominant and minor phyla. The use of inorganic fertilizers could also affect soil microbial biomass. Abbasi and Khizar (2012) reported a decrease in microbial biomass with the addition of inorganic fertilizer. In addition, a decrease in urease activity, P availability and functional bacterial phoD gene community involved in soil P cycling was found in soils with long-term chemical fertilization (Gautam et al., 2020).

In view of the deepening ecological and climate crises, the increasing demand for healthy food and the preservation of biodiversity, it should be noted that agriculture should undergo a transformation towards maintaining the balance of nature and producing healthy food. One of the most predicted strategies is the use of biofertilizers based on microorganisms, which show great potential for improving crop quality and soil health (Thomas, Singh, 2019).

BIOFERTILIZERS

Microbes that contribute to improved plant growth play a very important role in regulating the dynamics of various processes such as decomposition of organic matter, uptake of various plant nutrients such as nitrogen, phosphorus, potassium and also iron and magnesium (Lalitha, 2017). It is now widely accepted that bioinoculants are one of the key components of integrated plant nutrition management that can lead to sustainability. Furthermore, these microbial inoculants can be used as a cost-effective input to increase crop productivity by reducing mineral fertilizer application rates and ultimately harvesting healthier crops (Kour et al. 2020). Biofertilizer products, particularly those containing beneficial bacteria, can promote plant growth through the bacteria's ability to synthesise hormones and other compounds that help the plant absorb nutrients, increase root growth and improve water and nutrient uptake from the soil, other compounds: vitamins, VOCs – volatile organic compounds, exopolysaccharides and siderophores. Biofertilizers are an innovative approach to improving crop production and enhancing agricultural sustainability (Priya, Adhikary, 2020). Biofertilizers, also known as microbial inoculants, are essentially preparations of live cells or latent efficient microbial strains that aid plant nutrient uptake through association in the rhizosphere or phyllosphere. Active microbial strains can be applied to plant surfaces, seeds, soil or the rhizosphere (Kour et al., 2020).

The application of microbial preparations impacts the diversity, composition, and functional dynamics of microbial communities in soil, which has a substantial effects on soil microbiota. Compant et al. (2012) reported that biofertiliser use contributes to the relative growth of new functional groups of microorganisms as a result of interactions between biofertiliser strains and the native soil microbiome. Madhaiyan and Adhya (2014) indicate that microbial preparations positively influence plant health, soil fertility and nutrient cycling by supporting beneficial microbial taxa and their functions. According to Islam et al. (2016), biofertilisers can also improve soil structure, water retention and resistance to stressors by modifying the soil microbiota.

The beneficial interactions between PGPBs and plants can be divided into two categories. The first category includes microorganisms that directly promote plant growth (direct mechanisms) by contributing to plant nutrition (i.e. microorganisms that increase nutrient availability, e.g. atmospheric nitrogen-fixing bacteria, phosphate-solubilizing bacteria) and stimulating plant growth through the production of phytohormones (auxins, gibberellins, cytokinins). The second category includes microorganisms that promote plant growth and development indirectly (indirect mechanisms) by inhibiting the growth and/or activity of microorganisms that have pathogenic effects on plants. Such effects are referred to as biological plant protection (Woźniak, Gałązka, 2019) (Fig. 1).

Various microorganisms are important soil components and play a key role in many biotic processes in the soil ecosystem, maintaining the soil in an active state that allows for nutrient mobilization and long-term crop development. Biofertilizers containing plant growth promoting rhizobacteria (PGPR) are classified into groups based on their functions and mechanisms of action. The most commonly used biofertilizers are nitrogen fixers (N-fixers), potassium solubilizers (K-solubilizers) and phosphorus solubilizers (P-solubilizers) (Daniel et al., 2022).

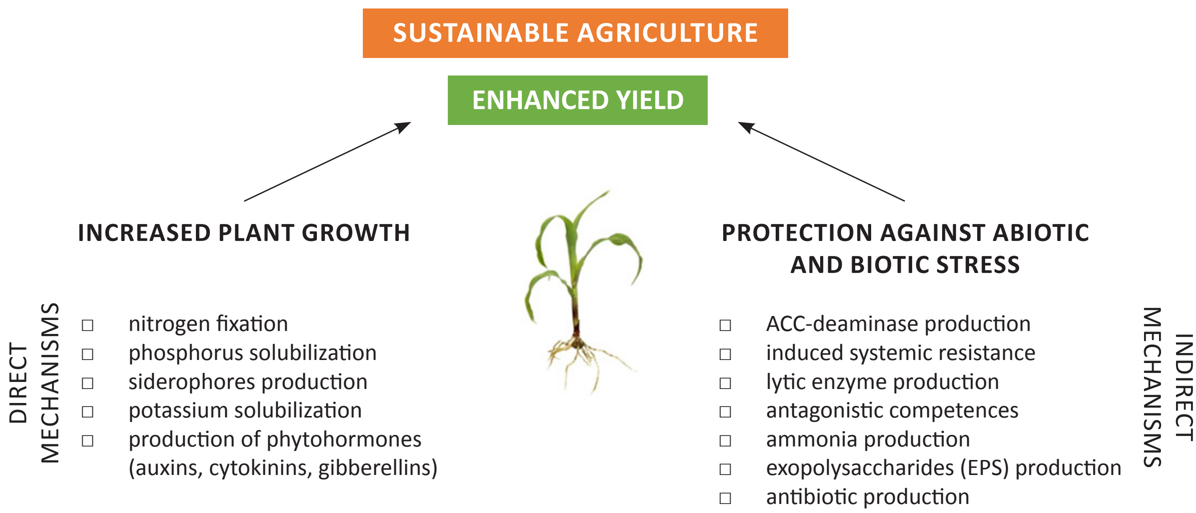

Figure 1. Mechanisms of plant growth promotion by microorganisms.

Nitrogen-Fixing Microbes

A number of micronutrients and macronutrients are required for proper plant growth, and deficiencies in any of these nutrients can lead to abnormal and unsustainable plant growth (Kumar et al., 2021). Nitrogen is one of the most important nutrients for plant growth and productivity. Although our atmosphere contains about 80% gaseous nitrogen, green plants are unable to use it directly (Daniel et al., 2022). Rhizosphere bacteria have a high potential for biological nitrogen fixation (BNF) of atmospheric nitrogen. In the natural environment, the process of biological N_2 fixation is one of the most efficient methods of introducing plant-available nitrogen compounds. The enzymatic conversion of molecular nitrogen to ammonia (the form of nitrogen assimilated by plants) is catalysed by nitrogenase, highly conserved enzyme complex common to all diazotrophs – nitrogen-fixing bacteria (Łyszcz, Gałązka, 2016; Woźniak, Gałązka, 2019).

Among nitrogen-fixing microorganisms, three groups can be distinguished, i.e. (Fig. 2):

(1) symbiotic nitrogen-fixing bacteria and other endophytic bacteria;
(2) asymbiotic bacteria living in the plant rhizosphere, the so-called associative bacteria;
(3) free-living bacteria inhabiting the soil.

Symbiotic bacteria are some of the best known atmospheric nitrogen-fixing bacteria and one of the most commonly used microorganisms in biofertilizers. They belong to the family *Rhizobiaceae* and consist mainly of genera such as *Allorhizobium*, *Azorhizobium*, *Bradyrhizobium*, *Mesorhizobium*, *Sinorhizobium* and *Rhizobium*. The root-nodule bacteria, known as rhizobia, are part of a well-known group of soil bacteria that, when coexisting with legume plants, cause the formation of root nodules on the plants where atmospheric nitrogen fixation takes place. In these symbiotic systems, free nitrogen is converted into a form that is available to the plant host (Łyszcz, Gałązka, 2016). In symbiotic systems, the nitrogen fixation efficiency reaches values from 200 to even 500 kg N_2 ha^{-1} $year^{-1}$ (Król, 2006). In this case, the microorganism is called a microsymbiont and the higher organism is called a macrosymbiont. The interdependence between the legume plants and the bacteria is a coexistence of two organisms from which both benefit. The microsymbiont converts atmospheric nitrogen into ammonia, providing ammonium nitrogen or glutamine to the plant tissues. In return, the plant host provides the bacteria with sugars and other substances produced during photosynthesis (Król, 2006; Łyszcz, Gałązka, 2016; Daniel et al., 2022). Inoculation of legume plants with a bacterial strain from the genus *Rhizobium* that exhibited 68% nitrogenase activity, resulting in a 16% increase in seed content (Glick, 2015). Co-inoculation of *Sinorhizobium meliloti* GL1 and *Enterobacter ludwigii* MJM-11 in a saline environment improves the alfalfa yield and nodule formation. Field experiment results also showed that after co-inoculation, the hay yield, crude protein and phosphorus content of alfalfa increased by 26.12%, 24.32% and 20.61% respectively (Gao et al., 2023).

Like rhizobia, **actinomycetes** of the genus *Frankia* fix atmospheric nitrogen in the root nodules of several woody

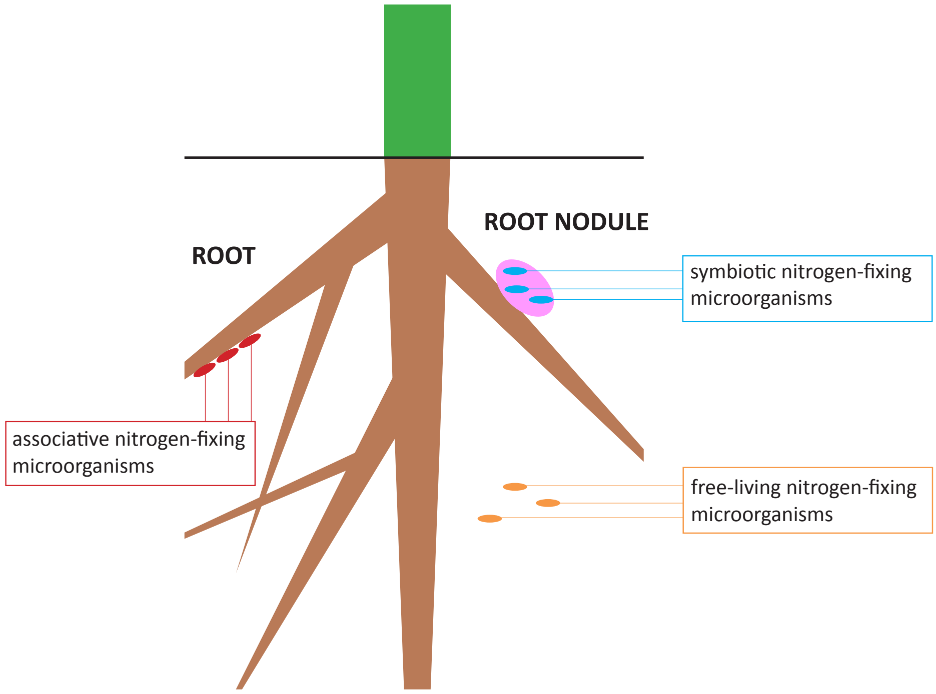

Figure 2. Groups of microorganisms fixing atmospheric nitrogen.

plants, e.g. *Casuarina*, *Alnus* (alder), *Myrica*, *Rubus*. Another ecologically important group of microorganisms that fix nitrogen in symbiosis are the blue-green algae (Cyanobacteria). They include *Trichodesmium*, *Tolypothrix*, *Nostoc* and *Anabaena*. These are photosynthetic organisms that contribute to about 36% of global nitrogen fixation and have been reported to help increase the fertility of rice fields in many parts of the world (Gallon, 2001; Thomas, Singh, 2019). According to Wang et al. (2015), several researchers have analysed the use of cyanobacteria as biofertilizers in rice cultivation in countries such as India, Japan, Philippines and Iran. Various studies have shown an increase in rice yield of up to 19.5%. In the study by Santini et al. (2022), cyanobacterial hydrolysates were reported to have biostimulatory activity on *Ocimum basilicum* L. grown hydroponically. Cyanobacterial hydrolysates effectively increased plant growth (up to +32%) and the number (up to +24%) and fresh weight (up to +26%) of leaves compared to controls.

Associative bacteria living in the rhizosphere of plants interact less closely with plants than symbiotic bacteria. The efficiency of N_2 fixation by free-living prokaryotes is low, ranging from about 1 to 50 kg N_2 ha^{-1} $year^{-1}$ (Król, 2006). These include *Gluconacetobacter diazotrophicus* and *Herbaspirillum* spp. associated with sugarcane, sorghum and maize (Luna et al., 2010; da Cunha et al., 2022), *Alcaligenes*, *Bacillus*, *Enterobacter*, *Klebsiella* and *Pseudomonas* species with rice and maize (James, 2000). One of the most well-described groups of free-living nitrogen-fixing bacteria is the genus *Azospirillum*. *Azospirillum* forms associative interactions with many plants, especially those with the C4 dicarboxylic acid pathway of photosynthesis (Mishra, Dash, 2014). These bacteria are most commonly used in biofertilizers for maize, sugarcane, sorghum, pearl millet and other crops (Daniel et al., 2022). Apart from nitrogen fixation, the main effects of plant inoculation with *Azospirillum* bacteria include changes in root morphology and synthesis of phytohormones, which ultimately improve plant growth (Fibach-Paldi et al., 2011). It has been reported that plant inoculation with *Azospirillum* bacteria has the potential to reduce nitrogen fertilizer use by up to 30–40 kg ha^{-1} (Fukami et al., 2016). Ardakani et al. (2011) showed that inoculation of wheat with *A. brasilense* strain increased the efficiency of nitrogen (~18%), phosphorus (~14%) and potassium (~20%) uptake. Studies conducted by Rajani et al. (2023) after inoculation of rice seeds with *Gluconacetobacter diazotrophicus* showed an increase in germination percentage (4.26–10%), germination time (3.8–5.8%) and germination rate (10.5–26.8%) compared to the control on agar medium after 5 days. In addition, inoculation resulted in a significant increase in growth parameters (i.e. root length, shoot length, root dry weight, shoot dry weight, seedling vigor index) in the five rice varieties compared to the non-inoculated control plants.

Among the **free-living soil bacteria with the ability to fix atmospheric nitrogen**, bacteria of the genus *Azotobacter* are the most commonly mentioned. These are non-symbiotic, free-living, aerobic, photoautotrophic bacteria belonging to the family *Azotobacteriaceae*. *Azotobacter chroococcum* is the most common species found in cultivated soils. These bacteria are sensitive to acid pH, high salt concentrations and temperature. They are usually found in neutral and alkaline soils (Moraditochaee et al., 2014; Daniel et al., 2022). *Azotobacter* spp. use atmospheric nitrogen to synthesise cellular proteins that are after bacteria death mineralized in the soil and then N is available to crops. These bacteria exert beneficial effects on crop growth and yield through their ability to synthesise biologically active compounds, produce phytopathogen inhibitors, modulate nutrient uptake (Lenart, 2012). Some reports suggest that *Azotobacter* has a fixation capacity of about 20 kg N ha^{-1} $year^{-1}$ and can therefore be successfully used in crop production as an alternative to at least some mineral nitrogen fertilizers (Sumbul et al., 2020). Furthermore, Romero-Perdomo et al. (2017) indicate that inoculating plants with a mixture of bacteria from the genus *Azotobacter* can reduce the need for nitrogen fertilizer by up to 50%. Ritika and Utpal (2014) evaluated that *Azotobacter* inoculation as N-biofertiliser increased the growth and yield of various crops under field conditions, with a percentage increase of up to 40% for cauliflower and 15–20% for maize compared to conventional fertiliser.

Phosphorus solubilizing microbes

Phosphorus (P) is one of the three essential macronutrients required for proper plant growth and development. Phosphorus is required by the plant from the seedling stage to full maturity – and has a measurable effect on the quality and quantity of the crop. At the molecular level, P is essential for many physiological and biochemical activities in plants, including ensuring proper photosynthesis, root and stem development, flower and seed formation. It is also a major component of DNA and RNA (genetic material) (Wang et al., 2023; Kour et al., 2020). Phosphorus accounts for 0.2 to 0.8 percent of plant dry weight and is a component of nucleic acids, enzymes, coenzymes, nucleotides and phospholipids (Kalayu, 2019). P concentrations in soil range from 400 to 1200 mg kg^{-1} soil. Despite the high total concentration, its soluble concentration is very low and unavailable to plants. The average phosphorus content in soil is about 0.05% (w/w), but only 0.1% of this phosphorus is available to plants. It is most abundant in the shallow soil layers and its content decreases with depth in the soil profile. It is present in the soil in two forms, inorganic and organic. The main mineral forms of phosphorus include hydroxyapatite, apatite and hydrated oxides such as iron, aluminium and manganese. Organic forms of phosphorus include dead microorganism, plant and animal matter. Soil phosphorus deficiency is often remedied by the application of phosphate fertilizers (organic and inorganic/mineral). Unfortunately, the effectiveness of applied mineral phosphate fertilizers is limited by their fixation as iron/aluminium phosphate in acidic soils or as calcium phosphate in neutral to alkaline soils. Furthermore, over-application of mineral fertilizers can contribute to environmental degradation (Wang et al., 2023; Kour et al., 2020; Kalayu, 2019; Woźniak, Gałązka, 2019; Siebielec et al., 2021).

One way to increase the availability of phosphorus to plants is to use biopreparations containing microorganisms with a high potential for mobilizing nutrients, such as phosphate solubilizing bacteria (PSB) and phosphate solubilizing fungi (PSF). Phosphate solubilizing microorganisms (PSMs) are a large group of microorganisms that mediate the bioavailability of phosphorus in soil and play a key role in the biochemical cycling of P in soil by mineralizing organic P, solubilizing inorganic P minerals and storing large amounts of P in biomass. These microorganisms are capable of solubilizing soil-insoluble phosphate and making it available to plants, thus contributing to environmental protection. PSMs are a group of beneficial microorganisms that inhabit the soil, rhizosphere, phyllosphere and endosphere of plants (Ibrahim et al., 2022). Of the total PSM microbial population found in soil, P-solubilizing bacteria account for 1–50%. Most PSMs have been isolated from the rhizosphere of various plants, where they are known to be most metabolically active (Chen et al., 2006; Khan et al., 2009). There is great diversity among PSMs (Shrivastava et al., 2018; Woźniak, Gałązka 2019; Siebielec et al., 2021; da Silva et al., 2023). The main mechanism for solubilizing inorganic forms of phosphorus is the ability of bacteria to synthesize low molecular weight organic acids, e.g. phenolic acid, citric acid and fumaric acid. In general, organic acids, when released, lower the pH and the phosphorus-bound cations are chelated by their hydroxyl and carbonyl groups. In addition, these acids can compete for P adsorption sites and form complexes with P-bound metal ions (Siebielec et al., 2021; Mander et al., 2012; Rawat et al., 2021; da Silva et al., 2023). Other mechanisms used by bacteria to solubilise phosphate include the production of inorganic acids (sulphuric acid, nitric acid and carbonic acid) and the secretion of other factors such as enzymes, exopolysaccharides, siderophores, protons, H_2S (Siebielec et al., 2021; Timofeeva et al., 2022a; da Silva et al., 2023).

Phosphorus mineralization refers to the solubilization of organic phosphorus and the degradation of the rest of the molecule. Several groups of enzymes secreted by phosphate solubilizing microorganisms are involved in phosphate mineralization. The first group of enzymes are the non-specific acid phosphatases (NSAPs). The best studied NSAP enzymes are phosphomonoesterases, also known as phosphatases. These enzymes are capable of phosphorylating a wide range of phosphoesters and solubilize about 90% of organophosphates in soil. Another enzyme produced by PSM in the mineralization of organic P is phytase. This enzyme is responsible for releasing phosphorus from organic matter in the soil (plant seeds and pollen), which is stored as phytate. The breakdown of phytates by phytase releases phosphorus in a form that is available to plants. Other enzymes involved in the mineralization of organic phosphorus include phosphate hydrolases and carbon-phosphate lyases. The above-mentioned enzymatic activity has been identified, among others, in bacteria of the genera *Pantoea*, *Pseudomonas*, *Enterobacter*, *Eschericha*, *Bacillus*, *Streptomyces*, *Janthinobacterium*, *Shewanella oneidensis*, *Burkholderia cepacia*, *Citrobacter freundii*, *Proteus mirabilis*, *Serratia marcescens* and *Klebsiella aerogenes* (Alori et al., 2017; Timofeeva et al., 2022a; da Silva et al., 2023).

The ability of PSMs to convert insoluble organic and inorganic phosphorus is closely related to soil characteristics. PSMs from soils with extreme environmental conditions, such as saline-alkaline soils, very nutrient-deficient soils or soils from extreme temperature environments, tend to dissolve more phosphate than PSMs from soils with more moderate conditions (Zhu et al., 2011). Other factors influencing microbial phosphate solubilization include interactions with other microorganisms in the soil, plant type, plant growth stage, ecological conditions, climate zone, agronomic practices, land use systems and soil physicochemical properties such as organic matter content and pH (Seshachala, Tallapragada, 2012). Phosphorus dissolves faster in warm, humid climates and slower in cool, dry climates. A well aerated soil is more conducive to phosphate dissolution than a moist soil saturated with water. Soils rich in organic matter promote microbial growth and therefore microbial dissolution of phosphorus (Alori et al., 2017).

Phosphorus solubilizing properties have been demonstrated for bacteria such as *Bacillus*, *Pseudomonas, Achromobacter*, *Brevibacterium*, *Burkholderia*, *Corynebacterium*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Rhodococcus*, *Serratia* and *Xanthomonas*. Cyanobacteria such as *Anabaena*, *Nostoc*, *Scytonema*, *Calothrix braunii* and *Tolypothrix ceylonica* have also been reported to dissolve phosphorus in soil. Among fungi, *Aspergillus*, *Paecilomyces*, *Penicillium*, *Sclerotium rolfisii*, *Cephalosporium* sp., *Alternaria* sp., *Cylindrocladium* sp., *Fusarium* sp., *Rhizoctonia* sp., *Rhodotorula minuta*, *Saccharomyces cerevisiae* and *Torula thermophila* can dissolve inorganic phosphates (Mishra et al., 2014; Kour et al., 2020). From literature data, phosphorus solubilizers including *Aspergillus*, *Bacillus*, *Escherichia*, *Arthrobacter* and *Pseudomonas* have been reported to add about 30–35 kg P_2O_5 ha^{-1} (Gaur et al., 2004). Research by Beltran-Medina et al. (2023) shows that inoculation of maize with *Rhizobium* sp. B02 improved shoot length and shoot dry matter (9.8 and 12%) and grain yield by 696 kg ha^{-1} using 50% of the recommended phosphorus fertilizer rate. Therefore, PSB inoculation can replace 50% of phosphorus fertilizer in maize and increase soil phosphorus availability. In the study by Wang et al. (2022), it was reported that wheat (*Triticum aestivum*) yield under PSB (*Pseudomonas moraviensis*, *Bacil-*

lus safensis and *Falsibacillus pallidus*) inoculation significantly increased up to 14.42% compared to the control on agricultural land where phosphate fertilisers were applied. In addition to promoting wheat growth, it was found that the labile P fraction in the soil significantly increased by more than 122.04% under PSB inoculation compared to soils without inoculation.

Potassium solubilizing microbes

After nitrogen (N) and phosphorus (P), potassium (K) is one of the most important macronutrients required for normal plant growth and development. K plays an important role in plant growth, metabolic and physiological processes (Soumare et al., 2022; Sharma et al., 2024). Plants require sufficient potassium for proper root growth and plant development. K facilitates grain filling and kernel development and also increases straw strength. It is involved in the activation of more than 60 different enzymes responsible for various plant processes including photosynthesis, metabolism of carbohydrates, organic acids, fats, nitrogenous compounds and starch synthesis. Potassium also plays a key role in increasing water use efficiency and regulating transpiration, thereby improving drought resistance and cold tolerance. Potassium is also involved in the detoxification of reactive oxygen species and provides resistance to biotic agents such as microbes and insect pests, which is well documented in the literature (Sattar et al., 2019; Johnson et al., 2022; Sharma et al., 2024).

Although potassium (K) is one of the most important macronutrients and the eighth most abundant element, accounting for about 2.1% of the Earth's crust, K uptake by plants is hindered (Bhattacharya et al., 2016). The total potassium content of soils ranges from 0.04 to 3% K, of which only 1 to 2% is available to plants (Sparks, Huang, 1985). The rest is bound to other minerals and therefore not available to plants (Sharma et al., 2024). Potassium occurs in the soil in several forms, including: mineral K, non-exchangeable K, exchangeable K and solution K. Depending on the soil type, mineral potassium accounts for about 90 to 98% of soil K, and most of this K is unavailable to plants. Minerals containing K are feldspar (orthoclase and microcline) and mica (biotite and muscovite). The form of potassium most readily taken up by soil microorganisms is potassium in solution. However, it should be noted that this is the form that is most susceptible to leaching in soil (Sparks, Huang, 1985; Sattar et al., 2019).

At present, the significant intensification of agriculture, the introduction of high-yielding crop varieties and hybrids, and the inappropriate use of nitrogen and phosphate fertilizers are depleting potassium reserves in soils. In addition, leaching, run-off and soil erosion also contribute to decreasing potassium levels. Unfortunately, the rapid depletion of potassium, combined with the lack of effective protocols for sustainable potassium supplementation, has made potassium deficiency one of the major constraints to crop production. On the other hand, excessive use of potassium fertilizers contributes to environmental degradation (Kour et al., 2020; Olaniyan et al., 2022; Sharma et al., 2024). Therefore, economical, but above all environmentally friendly and sustainable methods are needed to increase the bioavailability of this element in the soil with reduced use of mineral fertilisers. One possibility is to exploit the potential of plant-associated potassium-solubilizing microorganisms (KSMs). These have the unique ability to dissolve insoluble mineral forms of potassium. Therefore, inoculation of crops with KSMs in conditions of reduced rates of potassium fertilizer is a promising and environmentally friendly strategy to promote crop growth and development and reduce the use of mineral fertilizer (Sattar et al., 2019; Sharma et al., 2024; Mazahar, Umar 2022).

Microorganisms that contribute to increasing the bioavailability of potassium from K minerals use several mechanisms. Similar to P solubilization, the basic mechanism of K solubilization is the production of organic and inorganic acids and the production of protons (acidolysis mechanism). The presence of various organic acids has been reported in KSM such as oxalic acid, tartaric acid, gluconic acid, 2-ketogluconic acid, citric acid, malic acid, succinic acid, lactic acid, propionic acid, glycolic acid, malonic acid, fumaric acid, etc. The synthesis of acids lowers the pH of the soil and protonates potassium-containing minerals, causing them to dissolve. In addition, acids can also chelate Si^{4+}, Mg^{2+} and Ca^{2+} ions in complexes with K^+ in minerals, indirectly dissolving K and thus increasing its availability to plants (Olaniyan et al., 2022; Etesami et al., 2017; Sharma et al., 2024).

Microbial potassium solubilization also occurs through the ability of microorganisms to produce exopolysaccharides and form biofilms that are involved in mineral degradation and bioweathering processes, resulting in increased potassium release (Jini et al., 2023). In addition, increased potassium bioavailability is also attributed to redox reactions in which electrons are transferred from KSM to metal groups on mineral surfaces, resulting in degradation of the metal complex (Sharma et al., 2024).

KSMs are most commonly isolated from the rhizosphere of crops and soils rich in mineral forms of potassium. Potassium solubilizing bacteria (KSB) include *Acinetobacter pitti*, *Arthrobacter* sp., *Bacillus mucilaginosus*, *B. edaphicus*, *B. circulans*, *B. cereus, B. polymyxa*, *Cupriavidus oxalaticus*, *Paenibacillus mucilaginosus*, *P. amylolyticus*, *Rhizobium pusense* and species of *Achromobacter, Agrobacterium*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Micrococcus*, *Paraburkholderia*, *Priestia*, *Pseudomonas*, *Rhodopseudomonas* and *Sphingomonas*. Potassium-solubilizing fungi (KSF) include *Aspergillus terreus* and *A. niger*, *A. fumigatus*, *Glomus mosseae* and *G. intraradices*. In addition, yeast strains belonging to *Torulaspora globosa* and *Saccharomyces cerevisiae* have shown the ability to increase potassium bioavailability

(Bin et al., 2010; Zhao et al., 2023; Ghosh et al., 2023; Sharma et al., 2024). Similarly, Badr et al. (2006) showed that inoculation of sorghum with KSB increased dry matter yield by 48%, 65% and 58%; phosphorus uptake by 71%, 110% and 116%; and potassium uptake by 41%, 93% and 79% in clay, sandy and limestone soils, respectively. The results of the pot experiment showed that plant biomass and potassium content of *Mikania micrantha* with KSBS from the genus *Burkholderia* were higher than in the control without these bacteria (Sun et al., 2020).

Microbial enhancement of sulfur and iron acquisition of plants

Sulfur (S) is one of the essential macronutrients required for proper plant growth. It is involved in the synthesis of proteins, oils, vitamins and flavour-enhancing compounds. Sulfur deficiency in plants results in reduced photosynthetic activity, reduced nitrogen metabolism and protein synthesis, stunted growth, cause yellowing of young leaves and chlorosis, and ultimately poor yields (Chaudhary et al., 2022; Chaudhary et al., 2023). Some microorganisms have the unique ability to oxidise sulphur to a form of sulphate that plants can use, and these microorganisms are known as sulphur-oxidising bacteria (SOB). These include *Acidithiobacillus*, *Thiobacillus* and heterotrophic bacteria such as *Cytobacillus firmus*, *Enterobacter cloacae*, *Enterobacter ludwigii*, *Klebsiella oxytoca*, *Phytobacter diazotrophicus* and *Pseudomonas stutzeri* (Chaudhary et al., 2023). Many species of bacteria and fungi are capable of releasing S from sulphate esters via mineralisation catalysed by sulphatases, including arylsulphatase. In addition, microbes can also increase plant S nutrition through transcriptional regulation of the plant sulphate assimilation pathway (Singh et al., 2022). For example, the inoculation with SOB increased onion yield by 47–69% at different N rates (62, 124 and 248 kg ha^{-1}) compared to the uninoculated treatments (Awad et al., 2011). Studies conducted by Koźmińska et al. (2024) highlight the potential of SOB (*Halothiobacillus halophilus* and *Thiobacillus halophilus*) as beneficial microorganisms in increasing sulphur availability and improving tolerance of *Plantago coronopus* to moderate salt stress. SOB increased sulphur levels in almost all treatments, reduced toxic accumulation of sodium and chloride ions and increased potassium levels under drought and moderate salinity conditions.

Iron (Fe) is an essential micronutrient that plays a key role in plant growth. It is involved in metabolic processes in plants such as DNA and RNA synthesis, respiration and photosynthesis, oxygen transport, oxidative metabolism, cell proliferation, electron transfer. In plants, iron is involved in the synthesis of chlorophyll and is essential for maintaining the structure and function of chloroplasts. In addition, many metabolic pathways are activated by iron, which is a cofactor for many enzymes (Rout, Sahoo, 2015; Kroh, Pilon, 2020). The main symptoms of Fe deficiency in plants are leaf yellowing or chlorosis, impaired sugar metabolism, reduced adaptation to stress factors and, ultimately, low crop yields (Montero-Palmero et al., 2024). Microorganisms have developed a number of mechanisms to acquire this essential element and make it available to plants. These mechanisms include the uptake of iron bound to organic molecules such as citrate or haem, the uptake of iron by membrane-bound uptake systems and the synthesis of siderophores, which are secondary metabolites that capture iron from environmental sources by forming soluble Fe^{3+} complexes that are then actively taken up by specific receptors (Woźniak, Gałązka, 2019; Kramer et al., 2020). Bacteria producing siderophores belong to the genera *Azotobacter*, *Azospirillum*, *Bacillus*, *Dickeya*, *Enterobacter*, *Klebsiella*, *Kosakonia*, *Methylobacterium*, *Nocardia*, *Pantoea*, *Paenibacillus*, *Pseudomonas*, *Rhodococcus*, *Serratia*, *Streptomyces*, among others (Timofeeva et al., 2022b). Sultana et al. (2021) showed that *Bacillus aryabhattai* MS3, which produces iron chelating compounds, increased rice yield by 60 and 43% under salt-free and salt (200 mM NaCl) conditions, respectively. Wang et al. (2011) showed that siderophores produced by *Agrobacterium radiobacter* help to reduce soil As levels by about 54%.

BIOFERTILIZERS IN MARKET AND THEIR LIMITATIONS

The biostimulator market offers a wide range of preparations based on the above-mentioned groups of microorganisms (Table 1). In particular, nitrogen-fixing strains of the genera *Rhizobium*, *Azotobacter* and *Azospirillum* constitute the global market for biofertilizers (Yadav, Yadav, 2024). The global biofertilizer market was valued at USD 1.41 billion in 2024 and is anticipated to increase at USD 4.71 billion by 2034 and compounded annual growth rate of 12.83% between 2022 and 2027 (Biofertilizers..., n.d.). These data indicate significant market potential and growth opportunities for biofertilisers in the coming years.

Biofertilisers are an environmentally friendly complement to chemical fertilisers and other agrochemicals. In recent years, microbial formulations have gained importance in the quest for sustainable agriculture. Understanding the engineering of the rhizosphere and endosphere of plants can increase the efficiency of biofertilisers to provide maximum benefit to crops. A key element is to tailor biofertilisers to the specific needs of crops (Kour et al., 2020). The prospects for using microbial formulations are promising, offering a more sustainable and environmentally friendly approach to ensuring food security. However, there are limitations associated with biofertilisers (Mitter et al., 2021; Rai et al., 2023; Yadav, Yadav, 2024):

- the process of increasing nutrient availability by microorganisms is slower than that of mineral fertilisers; it does not provide the rapid supply of nutrients required by fast-growing plants, particularly at these key stages of growth;

Table 1. Randomly selected preparations from the world-wide market containing specific groups of microorganisms (Wykaz ..., n.d.).

Plant growth promote mechanism	Examples of preparations (microrganisms)
Nitrogen-fixing microbes	• Encera SC (*Gluconacetobacter diazotrophicus*) • Bacti-N (*Azotobacter* spp.) • bi azot (*Bacillus azotofixans*) • BlueN (*Methylobacterium symbioticum*) • AzotoPower (bacteria of the genus *Azotobacter* and *Arthrobacter*) • Nitragina (root-nodule bacteria e.g. of the genus *Rhizobium, Bradyrhizobium*)
Phosphorus solubilizing microbes	• bi fosfor (*Bacillus megaterium*) • FosfoPower (selected PSB strains) • BIOFOSFORIN (*Bacillus megaterium*) • Bacti-P (bacteria of the genus *Bacillus*)
Potassium solubilizing microbes	• BACYIV FIX (bacteria of the genus *Bacillus*, *Paenibacillus*, *Agrobacterium*) • Bacti-P (bacteria of the genus *Bacillus*) • BACILLUS VIP (bacteria of the genus *Bacillus*)

- the effect of preparations is largely dependent on environmental factors, e.g. temperature, soil pH, moisture, salinity; unfavorable conditions can significantly reduce the activity of microorganisms;
- competition with indigenous soil microorganisms can reduce the activity of biofertilizer-originated microorganisms and inhibit their proliferation;
- the stability of microbial strains; the efficacy of biofertiliser strains during storage and use is crucial for successful integration into agricultural practices;
- lack of adequate knowledge and training of farmers on the correct use and benefits of biofertilisers

SUMMARY

Improving plant and soil health using sustainable methods has become an urgent need due to climate change, environmental problems and the need to ensure food security for the world's population. In this context, the use of microorganisms with the ability to increase the availability and mobilization of key nutrients N, P, K is one of the most effective tools for biofertilization. Microorganisms with the ability to fix atmospheric nitrogen in root nodules and soil, microorganisms with the ability to solubilize and increase the mobilization of phosphorus and potassium, and which also have other PGP properties such as the production of phytohormones or protection against many biotic and abiotic stresses, are an important component of sustainable agriculture. Through a series of beneficial interactions between these microorganisms and the plant, they help to increase the quantity and quality of crops, improve soil structure and reduce the need for mineral fertilizers. In order to meet market and environmental needs, it should be emphasized that future research directions should focus on improving research techniques and selection of PGP microorganisms, as well as increasing social, environmental and economic awareness regarding the use of microbiologically enriched biofertilizer technology.

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