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Review

Microbially Enhanced Biofertilizers: Technologies, Mechanisms of Action, and Agricultural Applications

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Abstract: Intensive research has been conducted for many years to develop environmentally friendly techniques for plant cultivation that optimize the fertilization process. One of the most promising areas within the fertilizer industry is using microbiologically enriched fertilizers, which incorporate beneficial bacteria or fungi. Biofertilizers are the focus of studies on both their production technologies and their effects on crop growth and yield, presenting a potential alternative to conventional mineral fertilizers. The prolonged and improper use of mineral fertilizers, along with inadequate plant protection, a lack of organic fertilization, and poor crop rotation practices, negatively impact soil health, disrupting microbial populations and ultimately diminishing yield quality and quantity. Microorganisms, particularly specific groups known as plant growth -promoting rhizobacteria (PGPR) and beneficial fungi, are estimated to make up 85% of the total soil biomass and play a crucial role in soil fertility by mineralizing organic matter, suppressing pests and pathogens, forming humus, and maintaining proper soil structure. They also provide optimal conditions for plant growth. Soil microorganisms can be categorized as either autochthonous, naturally present in the soil, or zymogenic, which develop when easily assimilable organic matter is added. Key microorganisms such as *Micrococcus*, *Bacillus*, *Azotobacter*, and nitrogen-fixing bacteria like *Rhizobium* and *Bradyrhizobium* significantly contribute to soil health and plant growth. Microbially enhanced fertilizers not only supply essential macro- and micronutrients but also improve soil quality, enhance nutrient use efficiency, protect plants against pathogens, and restore natural soil fertility, fostering a balanced biological environment for sustainable agriculture.

Keywords: biofertilizers; beneficial microorganisms; plant growth-promoting bacteria; mycorrhizal fungi; nutrient use efficiency; sustainable agriculture

Academic Editor: Othmane Merah

Received: 18 March 2025
Revised: 23 April 2025
Accepted: 25 April 2025
Published: 15 May 2025

Citation: Figiel, S.; Rusek, P.; Ryszko, U.; Brodowska, M.S. Microbially Enhanced Biofertilizers: Technologies, Mechanisms of Action, and Agricultural Applications. *Agronomy* **2025**, *15*, 1191. https://doi.org/10.3390/agronomy15051191

1. Biofertilizers—Fertilizers Enhanced with Biologically Active Additives

Biofertilizer is a substance composed of biodegradable compounds and living organisms or their enzymatic products which, when applied to seeds, a plant's surface, or soil, colonizes the rhizosphere or inter-cellular spaces and stimulates plant growth by increasing the availability of basic nutrients for host plants [1]. Microbiological inoculants containing active microorganisms can be divided into different categories depending on their application; however, a precise definition of these products is lacking [2]. Nonetheless, the term biofertilizer refers to products containing one or more strains of useful soil microorganisms (bacteria or mycorrhizal fungi), increasing the availability and absorption of mineral fertilizers for plants in easy to handle and economic medium [3,4]. The term

biofertilizer was created by combining the word fertilizer with biological, implying the use of living organisms.

Biofertilizers can be classified based on the types of microorganisms they contain and their functional roles in plant nutrition:

1. Nitrogen-fixing biofertilizers: Containing microorganisms that can fix atmospheric nitrogen, such as *Rhizobium, Azotobacter, Azospirillum*, and cyanobacteria.
2. Phosphate-solubilizing biofertilizers: Containing microorganisms that solubilize insoluble phosphates, such as *Bacillus, Pseudomonas*, and *Aspergillus*.
3. Phosphate-mobilizing biofertilizers: Containing mycorrhizal fungi that help plants access phosphorus from soil.
4. Potassium-solubilizing biofertilizers: Containing microorganisms that release potassium from insoluble minerals, such as *Bacillus mucilaginosus* and *Bacillus edaphicus*.
5. Sulfur-oxidizing biofertilizers: Containing microorganisms that oxidize sulfur to make it available to plants, such as *Thiobacillus*.
6. Plant growth-promoting rhizobacteria (PGPR): Providing multiple benefits through various mechanisms, including hormone production, siderophore formation, and pathogen suppression [5].

The history of biofertilizers dates back to 1895, when the product Nitragin, *Rhizobia* bacteria grown in a laboratory and capable of fixing free atmospheric nitrogen and providing it to legume plants, was launched on the market by F. Nobbe and L. Hiltner. Scientific studies carried out by Nobbe and Hiltner were met with great interest and a new bacterial product became the object of field testing in different soils and on legume plant [6–8]. Biological fertilizers are very important for ecological agriculture as they support the creation of organic matter [9] and help to maintain the long-term fertility of soil, which ensures the production of safe and healthy food. This term very often refers to microorganism cultures that promote the growth of plants such as bacteria, fungi, or algae. It is important to note that biofertilizers can also be enhanced with enzymes, which serve as catalysts for various biochemical reactions in soil. These enzyme-enhanced biofertilizers can accelerate nutrient release from organic matter and improve overall nutrient cycling [10,11]

However, for applying the biological fertilizer in agricultural practice, active microorganisms must be placed in carrier materials, allowing them to be stored from the production period to application and effective provision to the soil or plant. It can be concluded from the above that the term biological fertilizer, similar to mineral or organic fertilizers, should refer to the product that is ready to be launched onto the market and is composed of useful microorganism strains contained in a carrier with additives that can increase the efficiency of the microorganism effect [3,4]. Active microorganisms are the most important components of biofertilizers, whereas the effectiveness of biofertilizers depends on the efficiency of the applied microorganisms [10].

Because of its chemical composition and chemical properties, the soil is a favorable environment for the development of variable microflora. Factors that are crucial for the development of microorganisms in soil include temperature (climatic conditions), pH, the availability of nutrients (fertility), humidity, and the structure of soil. The number of microorganisms in soil decreases with the distance from the surface, and they amount to null at a depth of 1–2 m. The largest group of microorganisms is present in soils, in the rhizosphere, and on the surface of roots. The most common groups of microorganisms present in the rhizosphere, stimulating the growth and development of plants, are bacteria (PGPR—plant growth-promoting rhizobacteria). PGPR are widely applied all over the world as a soil and plant modifier, which is very important for improving the condition of agricultural ecosystems, thanks to reducing the demand for chemical fertilizers and pesticides [11].

Rhizosphere bacteria are applied onto degraded soils as natural bio-filters, neutralizing and accumulating chemical contaminants of soil through mechanisms such as biosorption (the binding of pollutants to cell surfaces), bioaccumulation (intracellular accumulation), biotransformation (conversion to less toxic forms), and mineralization (the complete breakdown of organic compounds to inorganic substances). Examples include Pseudomonas species that can degrade petroleum hydrocarbons and Bacillus species that can immobilize heavy metals [12,13].

The pre-condition for classifying a particular group (type) of bacteria as PGPR is the ability to colonize the root and survive and reproduce in the rhizosphere of a particular plant, to compete with other microorganisms, and to stimulate plant growth [14]. The following bacteria are included as examples of PGPR: *Acetobacter*, *Achromobacter*, *Anahaena*, *Arthrobacter*, *Azoarcos*, *Azospirillum*, *Azotobacter*, *Bacillus*, *Burkholderia*, *Clostridium*, *Enterobacter*, *Flavobacterium*, *Frankia*, *Hydrogenophaga*, *Kluyvera*, *Microcoleus*, *Phyllobacterium*, *Pseudomonas*, *Serratia*, *Staphylococcus*, *Streptomyces*, *Vibri,* and others [15]. This list is not exhaustive, as many other bacterial genera have been identified with plant growth-promoting properties.

The use of PGPR is an effective method of increasing the volume of yields. Growth stimulation by PGPR is affected by indirect or direct mechanisms [16]. Direct mechanisms cover processes such as the solubilization of phosphates (mainly calcium, iron, or aluminum) into assimilable forms [17], fixation of atmospheric nitrogen, synthesis of phytohormones (such as auxin, cytokinins, and gibberellins), and formation of siderophores', HCN (hydrogen cyanide) and ammonia or vitamins. Indirect mechanisms are not involved directly in growth promotion, but they protect plants against phytopathogens. Indirect mechanisms include the production of antibiotics and enzymes degrading the cell walls, inducing systemic resistance (ISR), the synthesis of antifungal metabolites, and the activity of ACC (1-aminocyclopropane-1-carboxylate). Its effect involves lowering the level of ethylene, which has a negative effect on root development, thanks to the presence of 1-aminocyclopropane-1-carboxylate deaminase (ACC deaminase), degrading the precursor of ethylene biosynthesis [14].

This enzyme was identified in numerous soil bacteria, and it was found that it is very important for bacteria–plant interaction. It is not released outside the cell, but it is located in the microbe cytoplasm. The activity of ACC deaminase is different depending on the bacterial strain [18]. *Rhodococcus* and *Pseudomonas* bacteria show the highest activity [19]. Introducing the population of microorganisms that contain ACC deaminase and are capable of lowering ACC can be an effective method of improving the growth and development of plants sensitive to ethylene such as paprika, tomato, or rape [18].

Not all PGPRs are regarded as biofertilizers. The classification depends on their primary functional roles and mechanisms of action. While there is some overlap between different categories, not all PGPR strains perform all functions [15,16]. Plant growth-promoting bacteria used for combating plant disease, insects, and weeds are called biopesticides. For example, *Bacillus subtilis* or *Pseudomonas aureofaciens* prevent plant diseases by competing with their pathogens in the rhizosphere, by forming antifungal compounds and promoting the growth of plants and roots. Numerous cases have been identified where PGPR are used in both biofertilizers and biopesticides [1]. Strains of *Burkholderia cepacia* biologically control *Fusarium* spp. and they also stimulate the growth of maize in iron-deficient conditions by producing siderophores [20].

Microorganisms are also widely used beyond agriculture, including applications in the chemical, pharmaceutical, and food industries. One important group is composed of lactic acid bacteria (LAB), which play a crucial role in food preservation, particularly in silage production for livestock feed. LAB fermentation in silage creates acidic conditions

that inhibit spoilage microorganisms, preserve nutrients, and improve digestibility. This application demonstrates how the same microbiological principles used in biofertilizers can benefit other agricultural sectors [21,22].

Important factors regarding the technology of applying biofertilizers are as follows:

- The selection of the appropriate carrier;
- The application of a particular formulation type for inoculated products;
- The development of the appropriate application method [4,23]

The carrier constitutes the main part (by weight or by volume) of the inoculant and its function is to provide an appropriate number of active microorganisms promoting the growth and development of plants (PGPM—plant growth-promoting microorganisms) under good physiological conditions and at an appropriate time. This carrier should ensure an appropriate microenvironment for PBPM and sufficient durability of the product over time (at least 2–3 months at room temperature) [2]. Important characteristics affecting the selection of a carrier include having a standardized composition, ensuring chemical and physical stability, and containing the highest number of PGPM strains, as well as the possibility of mixing with other compounds (i.e., nutrients or adjuvants) [21]. If an inoculant is applied as a coating for seed treatment, the carrier should ensure the survival of PGPM on seeds, as usually, they are not sown immediately after being treated [22]. The durability of PGPM is very important for both the storage of the biofertilizer as well as after it is introduced into the soil [2]. Other important features of the carrier include a good capacity to absorb moisture, easy processing, sterility or easy sterilization by autoclaving or by other methods (e.g., gamma radiation), low cost, and availability [24]. The selection of a carrier specifies the physical form of the biological fertilizer. Carriers can be of organic, non-organic, and synthetic origin [2,25,26]. They can be categorized into four categories:

- Soil materials—peat, clay, coal, and lignite;
- Organic material of plant origin—charcoal, manure, cellulose, soybean pellets, soybean oil and nut oil, wheat bran, corncobs, and sawdust;
- Inert materials: bentonite, kaolin, silicates, vermiculite, perlite, calcium sulfate, and polyacrylamide gels;
- Freeze-dried microorganism cultures [27,28].

Combinations of various types of carriers are very common, such as soil and compost, or soil and peat [26]. For liquid inoculants, mineral and organic oils or oils suspended in water can be carriers [27]. While increasing microbial concentration in biofertilizers seems beneficial, it does not always result in proportionally positive effects on plant growth. High microbial populations can trigger intraspecific competition for limited resources, resulting in reduced efficacy. Additionally, certain microbial populations may produce metabolites that become inhibitory at high concentrations. Finding the optimal microbial concentration that balances efficacy with resource efficiency is crucial for biofertilizer development [28,29].

Biofertilizer formulation is a multi-stage process where one or more bacterial strains are interlinked to carriers and additives protecting cells during storage and transport [23,29]. The formulation process, when carried out properly, increases the number of bacteria in soil with a concurrent increase in their activity after being introduced to host plants [30]. The efficiency, durability, and price of the product depend on the formulation process. When considering microbial density in biofertilizers, it is important to note that increasing the colony forming units (CFUs) does not always correlate linearly with improved efficacy. Intraspecific competition can occur when microbial populations exceed certain thresholds, leading to reduced efficiency or even antagonistic effects. The optimal microbial concentration depends on the specific strains used, their interaction with the carrier material, and the target plant species. Therefore, formulation development should consider microbial popu-

lation dynamics to ensure sustained beneficial effects without triggering density-dependent negative interactions.

Four types of biofertilizer formulations are currently applied:

- Dry inoculants (powders): Dry inoculants are produced with the use of soil organic substances or inert carriers. Most frequently, the formulation of powder inoculants is carried out using peat. Peat ensures an environment that is rich in nutrients for the growth of a large variety of microorganisms. Peat should be non-toxic, highly adsorptive, and easily sterilized, and it should have a high content of organic matter and the capacity to absorb water, as well as being easily available at a reasonable price. The main drawback of peat is its variable composition. Peat inoculated with bacteria is usually introduced on seeds just before sowing [31,32].
- Liquid inoculants: Liquid inoculants are based on aqueous broth cultures in a polymer-based oil or water suspension. Liquid formulation gained great popularity because of the easy application of seeds into the soil [5,23]. Contrary to powder inoculants, the liquid formula allows the producer to include relevant amounts of nutrients and cell protection measures to improve the efficiency of bioproduct application [33]. Moreover, it was found that they do not contain impurities, and they are more field-efficient as compared to peat-based products [28]. Liquid inoculants require specific storage conditions (low temperatures) and have a limited durability time [34,35].
- Granules: Granules are made of peat lumps or marble, calcite and silicate grains coated or impregnated with microorganisms [29]. Granules have different sizes, but there is a correlation between the density of the matrix culture population and the quality of the final product [35]. Fertilizer granules are placed in furrows close to seeds to allow interaction between lateral roots, thanks to which they do not have direct contact with pesticides, which are toxic for microorganisms [23,26,30,34].
- Freeze-dried powders: Freeze-drying allows for obtaining a high bacteria survival rate without the necessity of using a carrier. To protect the cytoplasm and cell membranes of bacteria, cryoprotectants should be added, e.g., mannitol or microcrystal cellulose, which lead to slower degradation kinetics in soil and a higher stability of inoculums at room temperatures for a longer period [36].

The choice of bacterial carriers significantly impacts nitrogen and sulfur transformation processes in soil. Carriers not only physically protect microorganisms but also provide initial substrates for microbial metabolism. For instance, organic carriers like peat or compost may contain carbon sources that fuel microbial activity, potentially enhancing nitrogen fixation rates. Some carriers also create favorable microenvironments with appropriate pH, oxygen levels, and moisture that optimize enzymatic activities involved in nitrogen and sulfur transformations. Additionally, carrier surface properties affect bacterial attachment and colonization patterns, which influence how effectively bacteria interact with plant roots in the rhizosphere [33–35]. Biofertilizers should be stored in a cool place at room temperature (25–28 °C), away from heat sources and sunlight. Biofertilizers should not have direct contact with mineral fertilizers and pesticides, and expired biofertilizers should not be used in agriculture.

2. Legislation

On 25 June 2019, the new Regulation (EU) 2019/1009 of the European Parliament and of the Council was published, laying down the rules on the market for fertilizing products. The new regulation replaced Regulation (EU) 2003/2003 and covered all types of fertilizers and fertilizing products (Figure 1). It was a key part of the European circular economy framework, as it consolidated standards for fertilizers made from organic or secondary raw materials within the EU [37].

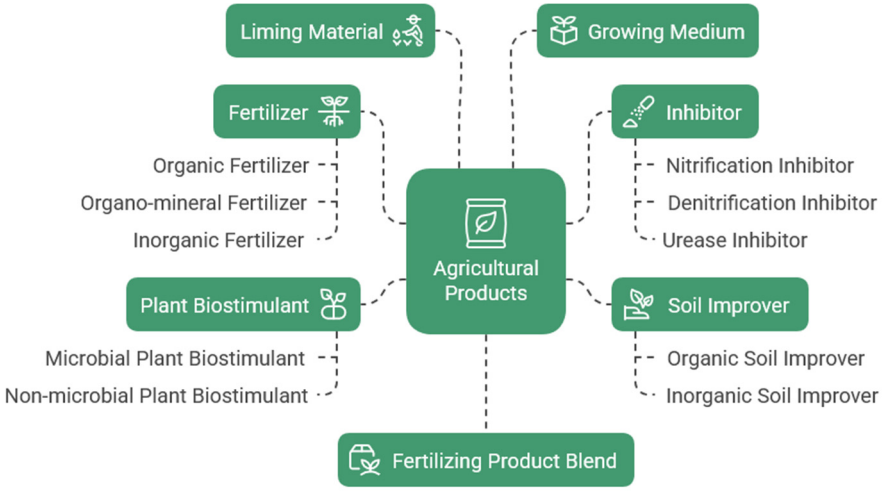

Figure 1. Classification of fertilizers and fertilizer products based on Regulation (UE) 2019/1009 of the 5 June 2019 [37].

The previous Regulation (EU) 2003/2003 primarily focused on mineral fertilizers and did not address innovative, microbiologically enhanced fertilizing products [38]. As a result, access to the market for these products was hindered due to the application of separate domestic regulations, which depended on mutual recognition between EU member states. Many microbiologically enhanced products were categorized as soil improvers rather than fertilizers for use in organic farming.

The new legal framework significantly eases the market access and use of organic fertilizers, as well as organo–mineral fertilizers, and those derived from plant or animal waste. According to the new provisions, fertilizers and fertilizing products that met European quality and safety standards were allowed on the EU market. These products could contain microorganisms (including dead or inactive ones) and harmless residues from the medium in which they were produced, provided they had undergone processes other than drying or freeze-drying. This included microorganisms like *Azotobacter* spp., *Rhizobium* spp., *Azospirillum* spp., and mycorrhizal fungi [37].

The regulation also created new opportunities for producing and selling fertilizers in line with the circular economy model here waste was converted into nutrients for plant cultivation. It expanded the range of available fertilizers and fertilizing products for farmers. The regulation entered into force 20 days after its publication in the Official Journal of the European Union and became applicable on 16 July 2022 [37,39].

3. Assimilation of Nutrients by Cultivated Plants

Understanding nutrient assimilation by plants is crucial for developing effective biofertilizers. The following sections examine how plants acquire and utilize key nutrients, and how biofertilizers can enhance these processes by increasing nutrient use efficiency (NUE). NUE is defined as the ratio between nutrient output (nutrient content in harvested crop) and input (nutrient applied) and is a critical parameter for evaluating fertilizer effectiveness. The effectiveness of nutrient uptake from different fertilizer types varies considerably based on environmental and biological factors. Conventional mineral fertilizers typically show immediate availability but may have lower overall efficiency due to losses through leaching, volatilization, and fixation in soil. Biofertilizers, by contrast, can enhance nutrient use efficiency through multiple mechanisms: the gradual release of nutrients, improved root architecture for better nutrient interception, enhanced soil structure for better nutrient retention, and the conversion of unavailable forms to plant-available forms. Key factors affecting fertilizer use efficiency include the following:

- Soil properties (pH, organic matter content, and texture);
- Environmental conditions (temperature and moisture);
- Microbial community composition and activity;
- Plant species and growth stage;
- Application method and timing.

Studies have shown that the combined application of mineral fertilizers with biofertilizers can increase nitrogen use efficiency by 10–25% and phosphorus use efficiency by 15–30% compared to mineral fertilizers alone. This synergistic effect represents one of the main advantages of integrated nutrient management strategies [40,41].

Soil nutrient resources can be divided into assimilable resources and total resources, inassimilable for cultivated plants. At the turn of the century, plant production was carried out with the use of soil natural resources and partial nutrient return in the form of organic fertilizers. Soil balance was maintained; however, the yield level was low. The fertilizer industry was developed in the nineteenth century, and it was related to the necessity of increasing plant production resulting from economic growth and rapid population increase. The total content of nutrients in soil depends on the natural properties of soil formation rocks; however, only small amounts are assimilable for plants. The assimilability of a nutrient specifies the amount of this nutrient which can be taken up by the plant not only from soil solution but also from the soil sorption complex and some slightly soluble salts [42]. The uptake of nutrients by plants is achieved by the root system and only to a low extent by leaves. For its growth and life activity, the plant needs mineral components in the appropriate amounts, chemical form, and specified time, resulting from the growth rate of plant organs and the cultivation purpose. These components are located in various mineral and organic substances in soil and fertilizers. Three groups of plant mineral nutrition are distinguished:

- Building elements: carbon, hydrogen, and oxygen, specified as biogenic elements;
- Macroelements: nitrogen, phosphorous, sulfur, potassium, calcium, and magnesium, present in soil and plants in the amount of 0.01–5.0%;
- Microelements: iron, manganese, zinc, molybdenum, boron, copper, chlorine and sodium, selenium, cobalt, and silicon—elements necessary for the proper development of only some plant species [14,42].

The concentration of microcomponents in plants is significantly lower than macrocomponents and ranges from 0.1 $mg \cdot kg^{-1}$ for molybdenum to 100 $mg \cdot kg^{-1}$ for iron or manganese [14].

In addition to their role in macronutrient cycling, soil microorganisms play crucial roles in the transformation and availability of micronutrients, particularly iron. Iron is essential for plant metabolism, including chlorophyll synthesis, respiration, and nitrogen fixation, yet it is often present in soils in forms unavailable to plants, especially in alkaline conditions.

Microorganisms enhance iron availability through several mechanisms:

1. Siderophore production: Many bacteria and fungi produce low-molecular-weight compounds called siderophores that chelate Fe^{3+} with high affinity, making them available for microbial and plant uptake. Key siderophore-producing microorganisms include *Pseudomonas*, *Bacillus*, and *Trichoderma* species.
2. Iron reduction: Some microorganisms can reduce Fe^{3+} to the more soluble Fe^{2+} form, facilitating plant uptake. Iron-reducing bacteria include *Geobacter* and *Shewanella* species.
3. Organic acid production: Similar to phosphate solubilization, the microbial production of organic acids can solubilize iron compounds by lowering pH and through chelation effects.

The application of iron-mobilizing microorganisms in biofertilizers has shown particular promise for crops grown in calcareous or alkaline soils where iron deficiency is common. Soil microorganisms are very important for chemical cycling in the natural environment [43–45].

3.1. Microbial Conversions of Nitrogen

Nitrogen is a vital, and the most yield-increasing, nutrient and one of the most important components of protein synthesis. The yield and the content of proteins in yields depend on nitrogen fertilization [42,46,47]. There is a constant mutual exchange of nitrogen in the environment. Free nitrogen enters the soil thanks to nitrification bacteria living on the roots of legume plants and by electrostatic discharge which results in the combination of N_2 and O_2, with the formation of NO which is then oxidized to NO_2. Nitrogen dioxide, NO_2, is dissolved in water, forming nitrates (NO_2^-) and nitrates (NO_3^-) which leach into the soil. The nitrogen cycle is in an insurable balance which can be locally disturbed by intensive soil cultivation. It is then necessary to supplement nitrogen by fertilization [48]. In non-fertilized soils, there is an insufficient amount of this element to satisfy the nutrient requirements of plants [42]. The majority of nitrogen conversions are biological and they occur under the effect of bacteria, fungi, and higher plants.

The nitrogen forms assimilable for plants include atmospheric nitrogen (N_2), ammonium ions (NH_4^+), and nitric ions (NO_3^-). The two last nitrogen forms are called mineral nitrogen (N_{min}) amounting to 1–5% of the total resources of nitrogen in cultivated soils. These forms constitute the most important part of nitrogen since they are directly taken up by plants. The remaining part covers organic nitrogen compounds present in variable forms, e.g., forms soluble in water: urea and some amino acids and humus forms: humus and dead organic matter which becomes assimilable for plants after microbiological conversion into mineral form [42,49].

The natural source of nitrogen for higher plants is molecular nitrogen. Unfortunately, the gaseous form of nitrogen (N_2) is not directly assimilable by living organisms. The phenomenon of nitrogen biological fixation occurs when atmospheric nitrogen is converted into ammonia by an enzyme called nitrogenase [50]. This process occurs in the presence of microorganisms containing this enzyme, including *Rhizobium* bacteria, which is the best known and which creates a symbiotic relationship with legume plants. A particular species of legume plant enters into symbiosis only with the selected species of rhizobia. The infection of rhizobia begins with the exchange of signaling molecules between the bacteria and its future host. The legume plants emit phenolic compounds, mainly flavonoids, which can diffuse through bacterial membranes [51,52]. Flavonoid signals induce nodulation gene expression, *nod*, and as a result, a low-molecular chitolipooligasaccharide is synthesized, called the Nod factor [53]. The emission of Nod factors to the soil environment leads to the induction of cell divisions of root bark which results in the formation of effective root nodules colonized by bacteria [49,51]. The formation of bacteroids is related to the formation of enzymatic complex nitrogenase [54]. This is composed of dinitrogenase with two cofactors, Fe and Mo, and dinitrogenase reductase with the iron–sulfur cluster 4Fe-4S, which provides dinitrogenase with electrons necessary for reduction [55]. Dinitrogenase is responsible for the six-electron reduction of N_2 [56]. The reduced ferredoxin is an electron donor. A high energy input is required, which is obtained from the decomposition of pyruvate. In the presence of Mg^{2+}, reductase forms a complex with an ATP of lower redox potential and it provides electrons to the appropriate nitrogenase. Dinitrogenase passes electrons to nitrogen molecules and it is capable of the fixation and reduction of N_2 [52] (Figure 2). Nitrogenase is very sensitive to oxygen and in its presence, it undergoes very fast and irreversible inactivation. Therefore, many microorganisms that fix nitrogen are

anaerobic, e.g., *Clostridium* [57]. The reduction of one molecule process of one N_2 leads to the formation of two molecules of ammonia and one molecule of gaseous hydrogen, and therefore, the reaction of nitrogen fixation requires eight electrons:

$$N_2 + 8e^- + 8H^+ + 16ATP \rightarrow 2NH_3 + H_2 + 16ADP + 16P_i \quad (1)$$

For the biological conversion of N_2 to NH_3, 16 molecules of ATP are required [52]. Hydrogen is quickly oxidized by hydrogen-oxidizing bacteria present in the cell [58,59], where ammonia released from the symbiosome is assimilated in plant cells leading to the formation of glutamine and asparagine. These amino acids enter non-infected cells and from there they enter the xylem [60,61]. Moreover, significant amounts of nitrogen compounds enter the soil from papillae and can be the source of nitrogen for other plants [62]. In return for the reduced nitrogen compounds, the plant provides its bacterial symbiote, carbon formed as a result of photosynthesis, which ensures the energy necessary for nitrogen reduction to the bacteroid [63,64].

While biological nitrogen fixation offers tremendous potential for sustainable agriculture, it also faces significant limitations. These include the following:

- Host specificity: Many nitrogen-fixing bacteria have narrow host ranges, limiting their applicability across different crops.
- Environmental sensitivity: Factors like soil acidity, temperature, and moisture significantly affect nitrogen fixation efficiency.
- Energy requirements: The process requires substantial energy from the plant, potentially reducing yield under certain conditions.
- Delayed nutrient availability: Unlike chemical fertilizers, biological nitrogen fixation provides nitrogen gradually over time.
- Competition with native soil microbiota: Introduced nitrogen-fixing bacteria must compete with established microbial communities.
- Variability in performance: Results can vary considerably across different field conditions and seasons.
- Establishment challenges: Successfully establishing symbiotic relationships in field conditions can be difficult [65,66].

The biological reduction of atmospheric nitrogen to ammonium ions assimilable by plants is used according to the assumptions of sustainable agriculture, which limits the use of synthetic nitrogen fertilizers, and it is carried out by bacteria called diazotrophs [65]. It is estimated that the maximum amount of nitrogen bound annually by the symbiotic bacteria varies from 100 to 700 kg/ha; therefore, this process is of great importance for nitrogen balance in soil [52]. Non-symbiotic rhizobia, which fix the atmospheric nitrogen, are also called diazotrophs and can enter into relationships with non-legume plants [66].

Microorganisms capable of reducing atmospheric nitrogen cover 87 species representing 38 types of bacteria, 20 types of cyanobacteria, and two archaea [14]. Nitrogen fixation bacteria can be divided into the following groups:

- Symbiotic bacteria, including *Rhizobiaceae* (*Rhizobium*, *Bradyrhizobium*, *Sinorhizobium*, *Azorhizobium*, *Mesorhizobium*, and *Allorhizobium*) [67]. Approx. 20% of legume plants are capable of entering into symbiosis with microorganisms, as a result of which molecular nitrogen is reduced and it is incorporated into the plant's metabolism. *Actinobacteria Frankia* living symbiotically with approx. 170 tree plants, mainly *Betulaceae*, fix approx. 10–200 kg N/ha [68].
- Non-symbiotic bacteria (free-living, associative, and endophytic), e.g., *Acetobacter*, *Herbaspirillum*, *Azoarcus* spp., *Alcaligenes*, *Azospirillum*, *Bacillus*, *Enterobacter*, *Klebsiella*, *Pseudomonas*, *Azotobacter*, *Burkholderia*, *Beiferinckia*, *Clostridium*, *Serratia*, and

Erwinia [69]. Non-symbiotic bacteria provide insignificant amounts of nitrogen to the related plants [70].

- Cyanobacteria (blue-green algae)—*Aulosira*, *Trichodesmium*, *Anabaena*, *Cylindrospermum*, *Nostoc plectonema*, and *Tolypothrix*. The cyanobacterial nitrogen fixation by *Azolla-Anabena* bacteria was of key importance in rice cultivation until the end of the 1970's [71].

The assimilation of nitrate ions NO_3^- is a multi-stage process that runs in two cell sections: cytoplasm and plastids [14]. The assimilation process is preceded by nitrate reduction using two enzyme systems: nitrate reductase (NR) and nitrite reductase (NiR) [72]. In the first stage, NO_3^- ions are reduced to NO_2^- ions, due to the nitrate reductase present in the cytoplasm. The donor of electrons in this reaction is NAD(P)H (nicotinamide adenine dinucleotide phosphate). Nitrate reductase is an inducible enzyme, the synthesis of which is controlled exogenously by substrate Re (NO_3^-) at the level of gene expression [52].

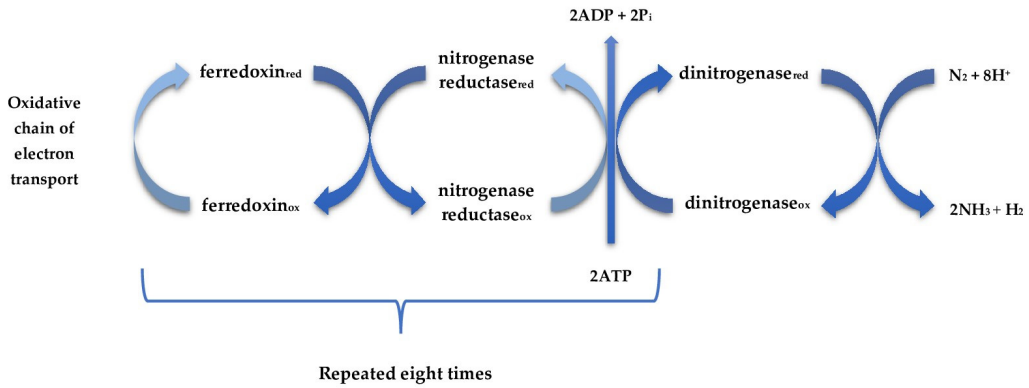

Figure 2. Mechanism of the nitrogenase complex [59].

The synthesis of this enzyme and its activity are limited by the following factors: NH_3, a low content of CO_2 in the air, a decrease in pH apoplast below 4.5, temperatures that are too low or high, a low content of water in the soil, and a lack of light [14], as its activity is controlled by light absorbed by phytochrome. In the first stage, NO_3^- ions are reduced to NO_2^- ions, due to the nitrate reductase present in the cytoplasm. The donor of electrons in this reaction is NAD(P)H (nicotinamide adenine dinucleotide phosphate).

$$NO_3^- + NAD(P)H + H^+ \rightarrow NO_2^- + NAD(P)^+ + H_2O \quad (2)$$

The toxic NO_2^- ions formed as a result of this process are transported to chloroplasts or plastids. In the second stage of assimilation reduction, nitrites are converted to ammonia with nitrite reductase, and the reduced ferredoxin or the plastids are electron donors. Ferredoxin reduction is related to the photosynthetic transport of electrons. Nitrite reduction is a process dependent on light, whereas, in non-photosynthetic tissues, ferredoxin is reduced by NADPH, which is a donor of electrons.

$$NO_2^- + 6Fd_{red} + 8H^+ + 6e^- \rightarrow NH_4^+ + 6Fd_{ox} + 2H_2O \quad (3)$$

The last stage involves the incorporation of NH_4^+ ions formed as a result of nitrate reduction or directly incorporated from the soil into the structure of amino acids [52]. This process is closely related to carbohydrate metabolism.

The major metabolites of nitrogen assimilation are glutamic acid and glutamic acid amide (glutamine). The three enzymes are involved in the formation of glutamine and glutamic acid: glutamate dehydrogenase (GDH), glutamine synthetase (GS), and glutamate synthase (GOGAT). Plants utilize two enzymatic pathways for amino acid biosynthesis

depending on the availability of assimilable nitrogen. Under nitrogen-rich conditions, the GDH-GS pathway predominates, whereas in nitrogen-deficient environments, the GS-GOGAT cycle is dominant [14]. The major mechanism of nitrogen assimilation in ammonium form is the glutamine synthetase—glutamate synthase (GS-GOGAT) cycle [73] (Figure 3). Approximately 90% of NH_4^+ ions are assimilated by plants through this cycle, which occurs in two enzymatic steps [52]. First, ammonium is incorporated into glutamic acid to form glutamine, a reaction catalyzed by glutamine synthetase (GS) with ATP (adenosine triphosphate) as an energy source. The presence of divalent metal ions, especially magnesium, is a necessary pre-requisite for the activity of the GS enzyme.

$$NH_4^+ + \text{glutamine acid} + ATP \overset{GS+\ Mg^{2+}}{\rightarrow} \text{glutamine} + ADP + P_i \quad (4)$$

In the second stage, the amide group from the formed glutamine is transferred by GOGAT, assisted by GS, onto α-ketoglutaric acid, leading to the formation of two molecules of glutamic acid. One of these molecules is re-incorporated into GS-GOGAT and the second undergoes further metabolic conversions in amino acid biosynthesis reactions. The source of α-ketoglutaric acid is the Krebs cycle [14].

$$\text{glutamine} + \alpha\text{-ketoglutaric acid} + NADPH \overset{GOGAT}{\rightarrow} 2\ \text{glutamine acid} + NADP^+ \quad (5)$$

The cycle of GS-GOGAT conversions is correlated with assimilations of other assimilable forms of nitrogen, e.g., urea, which after being assimilated to cells, is hydrolyzed in the cytoplasm by urease to carbon dioxide and ammonia [73]. Urea is not an ammonium fertilizer but it is an amide fertilizer. Plants can assimilate nitrogen from urea only after its hydrolysis to the ammonium form. Nitrogen release from urea increases with the soil temperature increase [42]. Urea can be decomposed by bacteria containing urease, e.g., *Bacterium vulgare*. Urea is intensely decomposed by bacteria with constitutive urease and its synthesis is not subject to repression by ammonia, e.g., *Bacillus pasteuri*.

$$CO(NH_2)_2 + 2H_2O \overset{urease}{\rightarrow} \uparrow 2NH_3 + H_2O + CO_2 \quad (6)$$

The formed ammonium ions can be transported to plastids and incorporated into the GS-GOGAT cycle or can be converted to glutamine by the isoform of glutamine synthetase (GS) and then to asparagine and glutamine acid, thanks to asparagine synthetase [73–75].

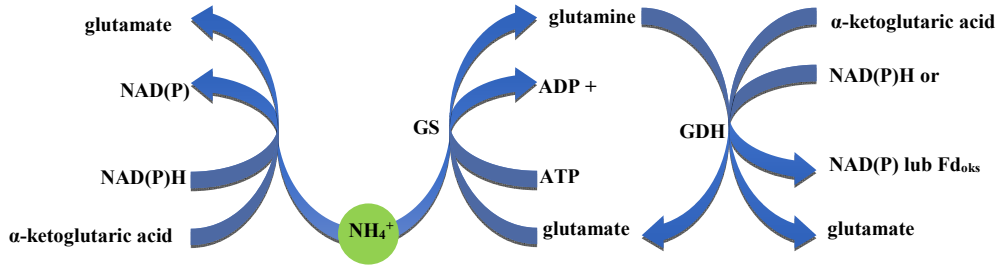

Figure 3. Mechanism of ammonium ions assimilation [75].

Despite their potential benefits, several factors limit the widespread adoption and effectiveness of nitrogen-fixing bacteria in commercial biofertilizers:

1. Host specificity: Many nitrogen-fixing bacteria, particularly rhizobia, have high host specificity, limiting their application to specific plant species or varieties.
2. Environmental sensitivity: Nitrogen fixation is inhibited by factors such as high soil nitrogen levels, low pH, drought, extreme temperatures, and oxygen exposure, making performance inconsistent across different agroecosystems.

3. Competition with indigenous microflora: Introduced nitrogen-fixing bacteria must compete with native soil microorganisms, often resulting in poor establishment.
4. Formulation challenges: Maintaining viability and activity during production, storage, and after application remains technically challenging.
5. Delayed benefits: Unlike mineral nitrogen fertilizers that provide immediately available nutrients, biological nitrogen fixation may take time to establish and provide significant amounts of fixed nitrogen.
6. Quantification difficulties: Measuring the actual contribution of biologically fixed nitrogen under field conditions is challenging, making it difficult to determine appropriate application rates.

Ongoing research focuses on addressing these limitations through improved strain selection, protective formulations, and integration with conventional fertilization approaches [13,76,77].

3.2. Microbial Conversions of Sulfur

Sulfur is one of the most important elements in plant nutrition present in soils in mineral and organic forms [42]. The sources of sulfur in cultivated soils are plant residues, atmospheric precipitation, and mineral and organic fertilizers. Although it amounts to only 1% of the cell weight, it is important for its proper development and functioning [78]. Sulfur is present in three chemical forms available for plants: sulfate anion SO_4^{2-}, sulfur dioxide SO_2, and hydrogen sulfide H_2S. The source of sulfur for cultivated plants is the soil where this element is assimilated as the sulfate anion SO_4^{2-}. The other gaseous forms of sulfur (SO_2 and H_2S) are assimilated marginally by leaves from the atmosphere. Thanks to their capability of taking and assimilating sulfates, plants are the most important producers of protein amino acids. Sulfates are reduced to thiol groups -SH, and sulfur is most frequently present in plants in this form. The reduction of SO_4^{2-} proceeds in chloroplasts and to a lesser extent in root plastids [52]. There is only one case known in *Euglena gracilis* where sulfur assimilation is affected in mitochondria [72]. The simplified pattern of reducing SO_4^{2-} to S^{2-} can be illustrated with the following reaction:

$$SO_4^{2-} + ATP + 8e^- + 8H^+ \rightarrow S^{2-} + 4H_2O + AMP + PP_i \quad (7)$$

Sulfur assimilation is a multi-stage process and it requires a huge metabolic energy input of the plant [68]. Sulfate assimilation resembles nitrate assimilation; however, the use of ATP in sulfate assimilation is five times higher [52]. The first stage of SO_4^{2-} reduction is activation, leading to the decrease in redox potential catalyzed by ATP sulfurylase [79], and to the active sulfate, i.e., adenosine-5′-phosphate (APS). The second substrate of this reaction is a molecule of high-energy ATP. Afterward, APS is reduced by APS reductase to sulfide (SO_3^{2-}). The source of protons is glutathione (GSH). The side reaction is APS phosphorylation, to be effected by APS kinase APS with the formation of (PAPAs) adenosine 5′-3′-phosphate (PAPS):

$$APS + ATP \rightarrow PAPS + ADP \quad (8)$$

In the subsequent stage, sulfide (S^{2-}) is reduced with sulfite reductase and with ferrodoxine as an electron donor. The last stage of the cycle is the conversion of sulfide into cysteine, with the cysteine precursor *O*-acetyloserine being involved in the process [80]. Cysteine is formed as a result of the effect of *O*-acetyloserine(thiol)lyase (OASTL) catalyzing the reaction that incorporates sulfide into *O*-acetyl serine (OAS) (Figure 4).

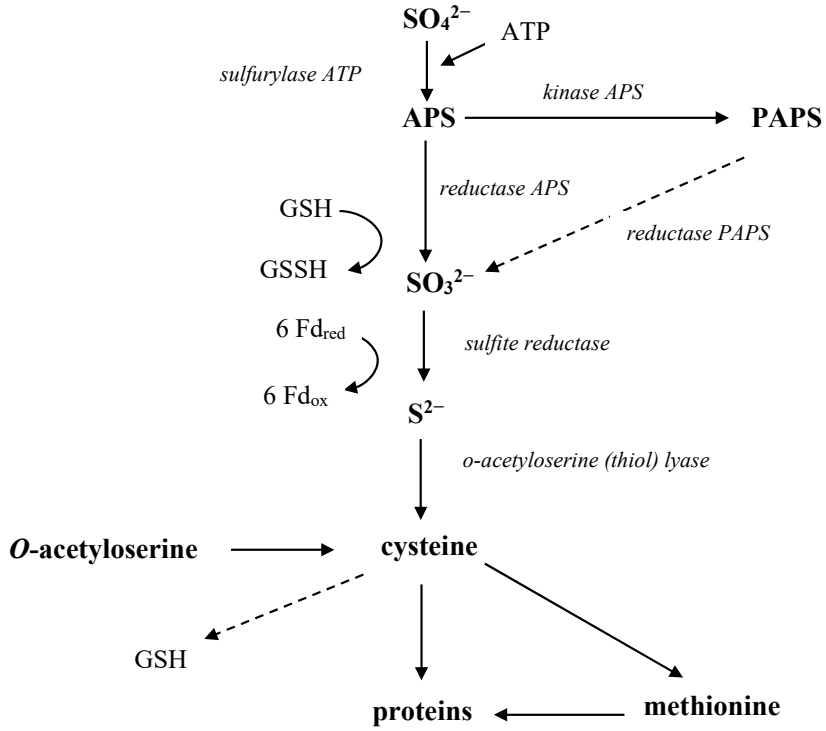

Figure 4. Assimilatory sulfate reduction in higher plants [14,80].

OAS, which is a donor of amino acid skeletons, is formed as a result of transferring the acetyl groups originating from acetyl-CoA onto serine with serine acetyltransferase (SAT). Cysteine is the first organic compound containing reduced sulfur and it is also the substrate for the production of glutathione (GSH), methionine, and other metabolites [81]. Methionine is formed in the reaction of cysteine with *O*-succinyl-homoserine catalyzed by γ-cystathionine synthase. Cystathionine is formed, which is converted by cystathionine β-lyase into homocysteine. This non-protein amino acid, which is a direct precursor of methionine, undergoes methylation in the presence of methionine synthase [82] (Figure 5).

Microorganisms have an important role in the microbial conversion of sulfur in soils. Non-organic sulfur compounds are used by bacteria for structural purposes. Most microorganisms assimilate sulfur in the form of sulfates, sulfites, and thiosulfates in the cysteine biosynthesis cycle where, using numerous enzymes, inorganic sulfur compounds are reduced and sulfur is incorporated into *O*-acetyl-serine with the formation of L-cysteine. This mechanism has been thoroughly studied in *Escherichia coli* and *Salmonella enterica* [83]. Moreover, some microorganisms can assimilate sulfides and, less frequently, elemental sulfur, e.g., *Acidithiobacillus ferrooxidans* or *Acidithiobacillus thiooxidans*, which are capable of oxidizing sulfur thanks to dioxygenase. Sulfur conversion to sulfite is catalyzed by sulfur dioxygenase. The SO_3^{2-} sulfite formed out of this process is incorporated into cysteine biosynthesis [84].

Methionine is formed in the reaction of cysteine with *O*-succinyl-homoserine catalyzed by γ-cystathionine synthase. Cystathionine is formed, which is converted by cystathionine β-lyase into homocysteine. This non-protein amino acid, which is a direct precursor of methionine, undergoes methylation.

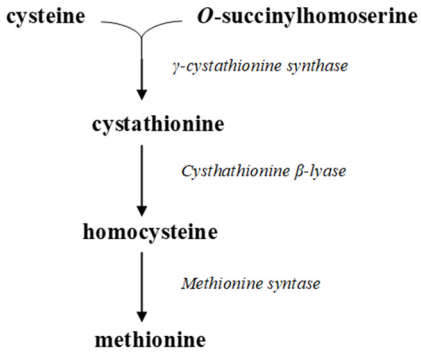

Figure 5. Biosynthesis of methionine [85].

3.3. Phosphorus Availability and Its Role in Plant Nutrition: Mechanisms of Assimilation and Solubilization by Microorganisms

Phosphorus is the second most important nutrient, except for nitrogen [86]. A key function of phosphorus, apart from its presence in numerous important compounds (phospholipids, nucleic acids, nucleotides, and co-enzymes), is its role in energetic conversions and the control of enzyme activity by its phosphorylation or dephosphorylation [58]. The great importance of phosphorus in the accumulation and transfer of energy results from the easy incorporation and transfer of electrons by this element. Adenosine-5-triphosphate (ATP) is the major carrier of energy in the cell.

An insufficient availability of phosphorus and potassium for plants reduces nitrogen utilization and leads to a drop in yield [87]. Contrary to nitrogen, phosphorus is sparsely diffused in soil. It is acknowledged that it remains on the layer of soil on which it has been applied with fertilizers [18]. It is found in organic and inorganic forms in soils [86]; however, for plants it is unavailable in organic form [18]. It is present in three forms in soils depending on its availability for plants:

- Active phosphorous present in soils as PO_4^{3-}, HPO_4^{2-}, and $H_2PO_4^{-}$, which are three levels of the dissociation of orthophosphoric acid;
- Assimilable phosphorous—tricalcium phosphate, iron phosphate, aluminum phosphate, dicalcium phosphate, dimagnesium phosphate, and vivianite—$Fe_3(PO_4)_2 \cdot 8H_2O$;
- Auxiliary phosphorous, which involves apatites—$Ca_{10}(PO_4)_6$ (OH^- or F^-)$_2$, variscite—$AlPO_4 \cdot 2H_2O$, and strengite—$FePO_4 \cdot 2H_2O$ [88].

Phosphorus is assimilated by plants in the form of the most oxidized inorganic compounds, i.e., orthophosphates [89]. $H_2PO_4^-$ and HPO_4^{2-}, and unlike nitrogen, it is not reduced in plants [52]. Pyrophosphates and metaphosphates are available for plants only after hydrolysis [89].

In slightly acid soils (pH > 5), phosphorus is present as $H_2PO_4^-$ anions and it is easily assimilable by plants from the soil. In an acidic environment, $H_2PO_4^-$ is converted into compounds that are not easily assimilable by plants, e.g., $AlPO_4$, $Fe_3(PO_4)_2$, and $FePO_4$, leading to a reversal of phosphorous. In an alkaline environment, HPO_4^{2-} ions are predominant in soil. Taking into account the availability of phosphorus for plants, the optimal pH of soil is 5.5–7.2. This optimal range represents the balance point where phosphorus is neither strongly bound to aluminum and iron oxides (as in acidic soils) nor precipitated with calcium (as in alkaline soils). Additionally, this pH range supports optimal microbial activity, including phosphate-solubilizing microorganisms, creating a priming effect where microbial metabolites further enhance phosphorus availability and plant growth [90–92].

The increase in soil pH leads to an increase in the dissociation of orthophosphoric acid, leading to a decrease in the assimilable form of phosphorous. In slightly acidic soils

(pH > 5), phosphorus is present as $H_2PO_4^-$ anions and it is easily assimilable by plants from the soil. In an acidic environment, $H_2PO_4^-$ is converted into compounds that are not easily assimilable by plants, e.g., $AlPO_4$, $Fe_3(PO_4)_2$, and $FePO_4$, leading to a reversal of phosphorous. In an alkaline environment, HPO_4^{2-} ions are predominant in soil. Taking into account the availability of phosphorus for plants, the optimal pH of soil is 5.5–7.2. The content of assimilable phosphorus ranges from 400 to 1200 $mg \cdot kg^{-1}$ [93] with only 1 mg/kg being available for plants as HPO_4^- and $H_2PO_4^{2-}$ [94]. The availability of inorganic phosphate in soils seriously limits plant production, and that is why this deficiency is corrected using phosphorus fertilizers. The uptake of phosphorus by plants is 10–20% [18]. The remaining phosphorus is quickly converted into insoluble complex compounds [53]. The assimilability of inorganic phosphorous compounds depends on soil pH, the content of calcium, iron, and aluminum, and on the content of organic matter as well as the presence of carbon dioxide in soil and its humidity and microbial activity [89]. Soil microorganisms, which activate insoluble mineral forms of phosphorus and which mineralize organic forms, are called *phosphate-solubilizing microorganisms*—PSMs [95]. PSMs constitute 10% of soil microorganisms [96]. This group includes both bacteria (*phosphate-solubilizing bacteria*—PSB), and some fungi (PSF—*phosphate-solubilizing fungi*) [97]. It is thought that PSB is more efficient in phosphorous solubilization than PSF [98]. Bacteria capable of solubilizing inorganic phosphorous are *Azotobacter*, *Bacillus*, *Beijerinckia*, *Burkholderia*, *Enterobacter*, *Erwinia*, *Flavobacterium*, *Microbacterium*, *Pseudomonas*, *Rhizobium*, and *Serratia* [71]. The mechanism of the solubilization of phosphates by PSB involves the production of organic acids which lower soil pH and facilitate phosphorus release such as gluconic acid (*Rhodococcus erythropolis* and *Phyllobacterium myrsinacearum*), citric acid (*Chryseobacterium* and *Serratiamarcescens*), malic acid (*Pseudosomonas* spp. and *Bacillus megaterium*), succinic acid (*Delftia* and *Pseudosomonas trivialis*), lactic acid (*Arthrobacter sp.* and *Azotobacter*), oxalic acid (*Pseudosomonas* spp. and *Azotobacter*) or fumaric acid (*Enterobacter*), and inorganic acids, e.g., sulfuric acid (*Thiobacillus ferrooxidans* and *Acidithiobacillus thiooxidans*) [99–101]. Moreover, low-molecular organic acids containing carboxyl or hydroxyl groups can chelate iron cations, calcium cations, and aluminum cations fixed with phosphates [102]. The type of generated acid and its amount depends on the type of microorganism. It was found that dicarboxylic and tricarboxylic acids are more efficient in phosphorous solubilization compared to single proton and aromatic acids, and aliphatic acids are more effective as compared to phenolic, citric, and fumaric acids [10].

While PSMs show significant potential for improving phosphorus availability, several limitations affect their effectiveness in field conditions:

1. Soil pH-buffering capacity: Highly buffered soils may neutralize the organic acids produced by PSMs, reducing their effectiveness in phosphate solubilization.
2. Variable performance: The efficiency of PSMs varies considerably depending on soil type, environmental conditions, and crop species.
3. Persistence issues: Many introduced PSMs show poor survival and colonization in field soils, particularly under stressful conditions.
4. Compatibility challenges: Some PSMs may not function optimally when combined with certain pesticides or other agricultural inputs.
5. Formulation stability: Maintaining viable populations of PSMs with consistent phosphate-solubilizing activity throughout the production, storage, and application process remains challenging.
6. Limited understanding of consortia effects: The interactions between different PSM strains and with other soil microorganisms are not fully understood, making it difficult to predict performance in complex soil environments.

To overcome these limitations, current research focuses on selecting robust, multifunctional PSM strains, developing protective formulations, and integrating PSMs into comprehensive soil management strategies [103–105].

Currently, numerous studies on the use of PSB are focused on the recovery of phosphorous from different types of materials such as sewage [106], sewage sludge ashes [107–109], bone meal, and bones [97]. Bones and sewage sludge ashes contain approx. 20% P_2O_5 after the third degree of purification and many valuable components for plant fertilization [110]. In addition to phosphate-solubilizing bacteria, mycorrhizal fungi play a crucial role in enhancing phosphorus availability to plants. Mycorrhizal symbiosis is a mutualistic association between plant roots and certain soil fungi, where the fungus provides the plant with nutrients, particularly phosphorus while receiving carbon compounds from the plant. The two main types of mycorrhizal associations are as follows:

- Ectomycorrhizae, where the fungal hyphae form a mantle around the root surface and penetrate between cortical cells but do not enter them. Common ectomycorrhizal fungi include species from the genera Amanita, Boletus, and Tuber.
- Endomycorrhizae, where the fungal hyphae penetrate the cell walls of the root cells. The most common type is arbuscular mycorrhizal fungi (AMF), which form arbuscules (tree-like structures) within root cortical cells. AMF belong to the phylum Glomeromycota and include genera such as Glomus, Gigaspora, and Acaulospora.

- Mycorrhizal fungi enhance phosphorus uptake through several mechanisms:
- The extension of the root system through external hyphae, increasing the soil volume explored by up to 1000 times;
- The production of phosphatase enzymes that hydrolyze organic phosphorus compounds;
- The secretion of organic acids that solubilize mineral phosphates;
- More efficient phosphorus uptake due to higher affinity transport systems.

Studies have shown that mycorrhizal fungi can increase phosphorus uptake by 3–5 times compared to non-mycorrhizal plants, leading to improved plant growth and yield, particularly in phosphorus-deficient soils. The effectiveness of mycorrhizal symbiosis depends on various factors, including fungal species, plant host, soil properties, and environmental conditions.

Biofertilizers containing mycorrhizal fungi are becoming increasingly popular in sustainable agriculture. These products typically contain spores or propagules of selected mycorrhizal fungi species, sometimes in combination with other beneficial microorganisms like phosphate-solubilizing bacteria, creating synergistic effects for improved plant nutrition.

3.4. Microbial Conversions of Potassium

Potassium is the third most important macronutrient necessary for normal plant growth and development, after nitrogen and phosphorus. However, unlike these elements, it occurs in plants mainly in ionic form and is not part of the organic compounds that build cells. It has key physiological functions, such as the regulation of water balance, the activation of more than 60 enzymes, participation in photosynthesis, protein synthesis, and the translocation of assimilates, and the regulation of the stomatal apparatus. An adequate supply of potassium to plants increases their resistance to biotic and abiotic stresses, including drought, salinity, low temperatures, and pathogen attacks. Potassium deficiency leads to lower yields and poorer crop quality, so maintaining adequate levels of available potassium in the soil is a key task in modern sustainable agriculture [111,112].

3.4.1. Forms of Potassium in the Soil and Their Availability to Plants

Potassium is one of the most widespread elements in the earth's crust, and its total content in soils ranges from 0.4% to 3%. Despite this relatively high content, only a small

proportion of soil potassium is directly available to plants. Potassium in soil occurs in four main forms:

- Potassium in soil solution—occurring as K^+ ions, directly available to plants, accounting for only 0.1–0.2% of total soil potassium content;
- Exchangeable potassium—adsorbed on the soil sorption complex, readily available to plants, accounting for 1–2% of total potassium content;
- Non-exchangeable potassium—trapped in the inter-packet spaces of clay minerals, hardly available to plants, accounting for 1–10% of the total potassium content [113];
- Structural potassium—embedded in the structure of primary (feldspars and mica) and secondary (clay minerals) minerals, practically unavailable to plants, accounting for 90–98% of the total potassium content of the soil [114].

The dynamic balance between these forms of potassium in the soil is crucial to the supply of this element to plants. As potassium is taken up by plants from the soil solution, it is replenished from the exchangeable potassium pool. When the exchangeable potassium content falls below a certain critical level, non-exchangeable potassium begins to be released, although this process is much slower [115].

3.4.2. Potassium-Solubilizing Microorganisms and Their Mechanisms of Action

Potassium-solubilizing microorganisms (KSMs) are a group of bacteria and fungi capable of converting unavailable forms of potassium into plant-available forms [116]. This process, known as potassium solubilization, is of particular importance in organic and sustainable farming systems, where the aim is to reduce the use of synthetic potassium fertilizers [117].

The most important potassium-solubilizing microorganisms include bacteria of the genera Bacillus (*B. mucilaginosus*, *B. edaphicus*, *B. circulans*, and *B. subtilis*), *Pseudomonas*, *Acidithiobacillus ferrooxidans*, *Paenibacillus*, *Arthrobacter*, *Enterobacter*, *Burkholderia*, and *Azotobacter* and fungi of the genera Aspergillus and Trichoderma [118,119]. These microorganisms occur naturally in the soil, especially in the rhizosphere of plants, where the availability of organic matter secreted by the roots favors their growth and activity [120].

Mechanisms of potassium solubilization by microorganisms include chemical, physical, and biological processes that lead to the breakdown of potassium minerals and the release of K^+ ions into the soil solution. The main mechanisms are as follows:

- Organic acid production—Microorganisms secrete a variety of organic acids such as citric, oxalic, tartaric, succinic, lactic, gluconic, and α-ketogluconic acids [121]. These acids lower the pH of the environment, which promotes the dissolution of potassium minerals. In addition, anions of organic acids can form complexes with cations (Ca^{2+}, Mg^{2+}, Fe^{3+}, and Al^{3+}) present in the crystal lattice of minerals, leading to their destabilization and the release of potassium [122].
- The production of chelating substances—Microorganisms secrete siderophores and other chelating compounds that bind metal cations in potassium minerals, leading to their breakdown and the release of potassium [123].
- The acidification of the environment—During respiration, microorganisms secrete CO_2, which forms carbonic acid (H_2CO_3) in soil solution, lowering the pH and increasing the solubility of potassium minerals [124].
- The production of extracellular polysaccharides (EPSs)—The polysaccharides secreted by microorganisms form a biofilm on the surface of potassium minerals, which promotes potassium solubilization by creating a microenvironment with reduced pH and an increased concentration of organic acids [125].
- The production of specific enzymes—Some microorganisms produce enzymes capable of catalyzing reactions that lead to the breakdown of potassium minerals [126].

- Redox reactions—Microorganisms can oxidize or reduce iron and manganese ions present in potassium minerals, leading to changes in the crystal structure and the release of potassium [127].

3.4.3. Biofertilizers Containing Potassium-Solubilizing Microorganisms

Biofertilizers are products containing live microorganisms that, when applied to seeds, plant surfaces, or soil, colonize the rhizosphere or interior of plants and stimulate their growth by increasing nutrient availability [1]. Biofertilizers containing potassium-solubilizing microorganisms are an important group of biofertilizers that can significantly improve the availability of this element to plants [128].

The effectiveness of potassium biofertilizers depends on several factors, such as the following:

1. The selection of suitable microbial strains: Effective strains should be characterized by high potassium solubilization capacity, resistance to unfavorable environmental conditions, the ability to colonize the rhizosphere, and a lack of antagonism towards other beneficial soil microorganisms [129].
2. Biofertilizer formulation: A suitable formulation should ensure the survival of the microorganisms during storage and application, facilitate their incorporation into the soil and stimulate their activity after application [2]. The most commonly used formulations are peat-based powders, granules, liquid formulations, and freeze-dried formulations [1].
3. Soil and environmental conditions: The effectiveness of biofertilizers depends on the physicochemical properties of the soil (pH, organic matter content, and cation exchange capacity), climatic conditions (temperature and humidity), and interaction with the autochthonous soil microflora [130].
4. The method and timing of application: The appropriate method of application (seed, soil, and foliar) and timing (before sowing or during the growing season) can significantly affect the effectiveness of a biofertilizer [28].

Studies in recent years have shown that the application of biofertilizers containing potassium-solubilizing microorganisms can lead to an increase in soil potassium availability by 15–40% and an improvement in crop yield by 10–30% [116,131]. Particularly promising results have been obtained for *Bacillus mucilaginosus* and *Bacillus edaphicus* strains, which have a high ability to solubilize potassium from aluminosilicate minerals [132].

Zhao and co-workers [133] showed that soil inoculation with *Bacillus mucilaginous* strain K02 increased soil exchangeable potassium content by 28% and improved maize yield by 18% compared to the control. Similar results were obtained by Meena and co-workers [134], who observed a 22–35% increase in soil potassium availability and a 12–20% improvement in wheat yield after the application of biofertilizers containing *Bacillus* spp. and *Pseudomonas* spp. strains.

Sheng and He [121] also conducted an interesting study, isolating and characterizing a strain of *Paenibacillus glucanolyticus* capable of solubilizing potassium from clay minerals. The authors showed that this strain's mechanism of potassium solubilization is mainly based on the production of oxalic and citric acids, which lower the environment's pH and form complexes with cations in potassium minerals. Soil inoculation with this strain led to a 31% increase in soil exchangeable potassium content and a 15% improvement in maize yield.

3.4.4. Interactions of Potassium-Solubilizing Microorganisms with Other Soil Microorganisms

Potassium-solubilizing microorganisms do not act in isolation, but are part of a complex soil ecosystem in which there are numerous interactions between different groups of microorganisms [135]. Studies have shown that there are synergistic interactions between potassium-solubilizing microorganisms and other beneficial soil microorganisms such as nitrogen-fixing bacteria, phosphorus-solubilizing microorganisms, mycorrhizal fungi, and plant growth-promoting bacteria [136].

Wu and co-workers [137] showed that a consortium consisting of a *Bacillus mucilaginosus* (potassium-solubilizing) and *Azotobacter chroococcum* (nitrogen-fixing) strain was more effective in increasing soil potassium and nitrogen availability and improving tomato yield than using these strains alone. Similar synergistic effects were observed for consortia of potassium- and phosphorus-solubilizing microorganisms [138].

Synergistic interactions between different groups of soil microorganisms may result from the following:

- The mutual supply of growth factors: Different groups of microorganisms can supply growth factors such as vitamins, amino acids, and nucleotides to each other [139];
- The removal of inhibitory metabolites: Some microorganisms can remove metabolites that inhibit the growth of other microorganisms [140];
- Changes in environmental properties: The activities of some microorganisms can lead to changes in environmental properties (pH and redox potential) that favor the growth of other microorganisms [125];
- The creation of functional systems: Different groups of microorganisms can form functional systems in which the metabolic products of some microorganisms are substrates for others [141].

3.4.5. Assimilation of Potassium by Plants Assisted by Microorganisms

Soil microorganisms, in addition to increasing the availability of potassium in the soil by solubilizing its unavailable forms, can also directly influence the processes of potassium uptake and assimilation by plants [142]. Studies have shown that some soil microorganisms, particularly from the PGPR group, can stimulate the expression of genes encoding potassium transporters in plant roots, thereby increasing the efficiency of the uptake of this element [143].

Potassium transporters in plants can be divided into several groups:

1. Shaker-type K^+ channels—potential difference-activated potassium channels, involved in the uptake of potassium from the soil at low external concentrations [144];
2. KUP/HAK/KT transporters—proton–potassium transporters, particularly important at low environmental potassium concentrations [145];
3. HKT transporters—potassium–sodium transporters, involved in potassium transport and the maintenance of ionic homeostasis under salt stress [146];
4. Antiporter-type K^+/H^+ transporters maintain the cell's potassium homeostasis [147].

Zhao and co-workers [148] showed that the inoculation of rice with a *Bacillus megaterium* strain increased the expression of genes encoding OsHAK1 and OsHAK5 transporters of the KUP/HAK/KT family, leading to an increase in the efficiency of potassium uptake by plants. Similar results were obtained by Wang and co-workers [149] for wheat inoculated with a *Bacillus subtilis* strain.

Soil microorganisms can also influence the assimilation of potassium by plants through the production of phytohormones (auxins, cytokinins, and gibberellins), which stimulate root growth and increase the absorption surface [69]. In addition, the production of siderophores by microorganisms can increase the availability of iron to plants, which

indirectly affects potassium metabolism, as iron is a component of numerous enzymes involved in the energy processes of the cell [141].

An interesting study was conducted by Liu and co-workers [150], who showed that the Bacillus subtilis BS-K strain stimulated potassium accumulation in lettuce plants under salt-stress conditions. The authors observed that inoculation with this strain increased the expression of genes encoding potassium transporters (LeHAK5 and LeAKT1) and proton pumps (LeHA1 and LeHA2), leading to increased K^+/Na^+ ratios in plant tissues and improved salinity tolerance.

3.4.6. Challenges and Prospects for the Use of Potassium-Solubilizing Biofertilizers

Despite promising results from laboratory and field studies, the wider use of biofertilizers containing potassium-solubilizing microorganisms faces some challenges and limitations:

- The variability of effects under different conditions—the effectiveness of biofertilizers can vary considerably depending on soil type, climatic conditions, plant species, and interaction with indigenous soil microflora [151];
- Microbial survival issues—maintaining microbial viability and activity during the production, storage, and application of biosolids is a significant technological challenge [29];
- Competition with indigenous microflora—introduced microorganisms must compete with natural soil microflora for ecological niche and substrates [152].
- A lack of quality standards—the lack of uniform quality standards and methods to assess the effectiveness of biofertilizers hinders their certification and marketing [28];
- Farmers' insufficient knowledge—a lack of knowledge and awareness among farmers about the benefits and proper use of biofertilizers limits their adoption in agricultural practice [35].

4. Impact of Carrier Materials on Microbial Nutrient Transformation Efficiency

The carrier materials used in biofertilizer formulations play a critical role beyond merely serving as physical vehicles for microorganisms. Research increasingly demonstrates that these carriers significantly influence microbial metabolic activities, survival rates, and nutrient transformation capabilities in agricultural applications. The selection of appropriate carrier materials represents a crucial factor in optimizing biofertilizer performance and enhancing soil fertility through microbial processes. Different carrier types create distinct microenvironments that can either enhance or inhibit specific microbial functions related to nutrient cycling. Organic carriers, including peat, compost, and plant residues, have been shown to provide additional nutrients and energy sources that stimulate microbial metabolism [153]. These materials can increase nitrogen fixation rates in diazotrophs by 15–30% compared to inert carriers, primarily due to the availability of carbon substrates that support microbial growth and activity. Recent studies on organic manure from biogas plants have demonstrated its effectiveness as a carrier material for various beneficial microorganisms, including *Azotobacter* sp., *Rhizobium* sp., and phosphate-solubilizing *Bacillus* sp., maintaining microbial viability for up to six months after production [154]. The structural properties of clay-based carriers confer significant advantages for microbial performance. These carriers can adsorb metabolic inhibitors and protect microorganisms from environmental stresses, potentially extending the period of active nitrogen fixation. Research on jasmine cultivation has shown that soil microbial populations and enzyme activities are significantly influenced by the nature of carrier materials used in nutrient delivery systems [155]. Clay materials create protective microhabitats that shield bacteria from predation and desiccation while maintaining favorable

moisture conditions for metabolic activities. Polymer-based carriers represent an innovative approach to biofertilizer formulation, offering controlled moisture conditions that optimize enzyme activities involved in phosphorus solubilization. Hydrophilic polymeric carriers can regulate water availability to microorganisms, creating stable conditions for enzymatic processes essential for nutrient transformation [156]. Studies with pelleted biofertilizers have demonstrated that combining appropriate carrier substances with co-inoculated bacteria and arbuscular mycorrhizal fungi significantly enhances their performance in rice cultivation [153]. The presence of trace elements in carrier materials is crucial in enhancing nutrient transformation pathways. For instance, molybdenum availability in the carrier can significantly enhance nitrogenase activity, the enzyme complex responsible for biological nitrogen fixation [157]. Recent advances in mixed microbial culture technologies have highlighted the importance of carrier-provided micronutrients in optimizing directional bio-synthesis and bio-transformation processes [158]. Biochar has emerged as a multifunctional carrier material with substantial benefits for microbial activity. Beyond its carbon storage capabilities, biochar serves as an effective nutrient and microbial carrier, creating favorable conditions for microbial proliferation and metabolic functions [159]. Its porous structure provides a habitat for microorganisms while adsorbing potential inhibitors that could otherwise limit nutrient transformation activities. However, certain carrier materials may contain compounds that inhibit microbial functions. Carriers with high phenolic content, often found in some composting materials, might inhibit key enzymatic activities involved in lignocellulose degradation and nutrient release [160]. Similarly, highly acidic carriers might suppress the growth of acid-sensitive microorganisms like *Azotobacter*, limiting nitrogen fixation potential in agricultural applications [153,154]. Recent research into *Rhizobium leguminosarum* as a biofertilizer has demonstrated that the efficacy of microbial inoculants depends significantly on the carrier substrate used. When appropriate carriers were employed, growth improvements ranging from 166.52% to 358.26% were observed in test crops, significantly outperforming conventional chemical fertilizers [161]. The development of liquid biofertilizer formulations represents another advance in carrier technology, offering improved shelf life and application efficiency compared to traditional solid carriers [162]. These liquid formulations maintain higher cell viability and metabolic activity, resulting in enhanced nutrient transformation upon soil application. Understanding the complex interactions between carrier materials and microbial communities is essential for optimizing nutrient cycling in agricultural systems [153,162]. The microbial potential for processes such as denitrification versus internal nitrogen cycling is significantly influenced by the physicochemical properties of the carrier environment, with implications for nitrogen retention and availability in agricultural soils [163]. The selection of appropriate carrier materials represents a critical factor in maximizing the nutrient transformation efficiency of microbial biofertilizers. Future research should focus on developing carrier formulations specifically tailored to enhance the metabolic capabilities of target microorganisms while protecting them from environmental stresses and inhibitory compounds.

5. Challenges and Limitations of Microbially Enhanced Biofertilizers

While microbially enhanced biofertilizers offer transformative potential for sustainable agriculture, their adoption faces significant challenges rooted in technical, regulatory, and practical constraints.

5.1. Regulatory and Quality Control Hurdles

Biofertilizer commercialization is hampered by fragmented regulatory frameworks, particularly in regions like India, where inconsistent standards and delayed approvals stifle innovation. Safety evaluations for microbial strains—including ecotoxicity assessments and

long-term environmental impact studies—are often inadequate, creating uncertainty for manufacturers and farmers. Additionally, quality control remains a critical issue, with many products lacking standardized metrics for microbial viability or nutrient content [164].

5.2. Technical Limitations in Strain Efficacy

Microbial strain stability under field conditions is a persistent challenge. Even robust laboratory-performing strains often fail to thrive in diverse soil ecosystems due to competition with native microbiota, pH fluctuations, or temperature extremes [165]. For example, *Pseudomonas fluorescens* PSM1, while effective in phosphate solubilization under controlled conditions, may show reduced activity in nutrient-poor or acidic soils. Multi-strain formulations designed to enhance resilience frequently face compatibility issues, leading to inconsistent crop responses.

5.3. Environmental and Application Risks

Improper application can negate biofertilizers' environmental benefits. Overuse may lead to nutrient leaching or unintended shifts in soil microbial communities, potentially exacerbating greenhouse gas emissions in waterlogged conditions. Furthermore, poorly characterized microbial consortia could introduce invasive species, though such risks remain understudied [165].

Practical challenges dominate on-ground implementation. Farmers report limited access to reliable products, delayed results compared to chemical fertilizers, and insufficient technical guidance. A 2024 survey highlighted that 65% of Indian farmers hesitated to adopt biofertilizers due to inconsistent yields and a lack of subsidies, despite recognizing their long-term soil health benefits.

5.4. Future Directions

Emerging strategies like rhizosphere engineering and CRISPR-based microbial tailoring show promise for enhancing strain adaptability. Policy interventions, including centralized certification systems and farmer education programs, are equally critical to bridge the lab-to-field gap. As research advances, integrating biofertilizers with precision agriculture technologies could address scalability and efficacy concerns, paving the way for broader adoption. This synthesis underscores the need for multidisciplinary collaboration to transform biofertilizers from a niche solution to a cornerstone of global agricultural sustainability.

6. Conclusions

Studies on the development of new cultivation and fertilization methods aim at producing high-quality yields and the protection of the natural environment. The necessity of introducing biofertilizers and useful microorganisms (bacteria and fungi) into agricultural practice results from the depletion or degradation of agricultural soils with a concurrent increase in production costs. The use of biologically enhanced fertilizers will increase the efficiency of the uptake and assimilation of nutrients by plants, and it will reduce the use of mineral fertilizers and plant protection products. It should be emphasized that despite the constant increase in bio-fertilizers in agriculture and gardening, this technology is still developing and evolving. The most important aspects to study, except for the identification of particular bacteria strains and their properties, are the mechanisms of biofertilizers and their efficiency in assimilating macro- and microelements for cultivated plants and their effect on plant growth and yield. Except for the above, the production technology should ensure the longest viability of microorganisms, i.e., the number of living cells, which is the most important parameter specifying the quality of these bio-products. Success related to the use of biological fertilizers depends on how the strategy correlates with the

functions of useful bacteria and their use in cultivated fields with more advanced and improved techniques.

Author Contributions: Conceptualization, S.F., U.R. and M.S.B.; writing—original draft preparation, S.F., P.R., U.R. and M.S.B.; writing—review and editing, S.F., P.R., U.R. and M.S.B.; visualization, S.F. and U.R.; supervision, P.R. and M.S.B. All authors have read and agreed to the published version of the manuscript.

Funding: The financial support for this study was provided within the Program of the Ministry of Science and Higher Education entitled the Industrial Doctoral Program under decision No. MEIN.WRC.23.239.RIO (SD.WRC.24.079.RIO).

Data Availability Statement: Not applicable.

Conflicts of Interest: The authors declare no conflicts of interest.

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