Microbial Fertilizers Regulate Crop Growth and Resistance

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Microbial fertilizer is a kind of nutrient-rich and environmentally friendly biological fertilizer made from plant growth-promoting bacteria (PGPR). Microbial fertilizers can regulate soil nutrient dynamics and promote soil nutrient cycling by improving soil microbial community changes. This process helps restore the soil ecosystem, which in turn promotes nutrient uptake, regulates crop growth, and enhances crop resistance to biotic and abiotic stresses.

Keywords: crop growth ; microbial fertilizers ; crop resistance

1. Introduction

Microbial fertilizer is a type of bio-fertilizer containing beneficial microorganisms with specific functions [1]. The application of microbial fertilizers can help the soil form a new microbial community structure and promote the supply of nutrients to plants with the soil [2]. Numerous studies have shown that microbial fertilizers made from PGPR play an important role in improving soil fertility and promoting crop growth. They also help crops combat biotic and abiotic stresses. Today, microbial fertilizers are considered renewable and environmentally friendly, supporting sustainable agriculture.

2. Microbial Fertilizers Regulate Crop Growth and Resistance

2.1. Microbial Fertilizers Regulate Crop Growth

Plant growth and development are intricately linked through mutual interactions between organisms in the root of plants and the rhizosphere. The rhizosphere prevails as a distinct habitat for the majority of microorganisms, serving as a direct source of their nutrients. In particular, bacteria that live around the roots, for example PGPR, are recognized as beneficial bacteria that promote plant growth and regulate plant growth and development. PGPR regulate plant growth and enhance yield via diverse direct action mechanisms, further augmenting plant nutrient assimilation [3]. The mechanisms of the direct action of PGPR encompass nitrogen fixation, the solubilization of phosphorus and potassium minerals, the generation of plant hormones, and the production of ferric iron carriers [4].

2.1.1. Nitrogen Fixation

Nitrogen is a critical nutrient element in the growth and development of plants. As the nitrogen in the atmosphere exists in its free state, most plants are incapable of directly utilizing it. Thus, the necessity arises to fix the free nitrogen and transmute it into nitrogen that can be absorbed and utilized by plants. Significantly, a plethora of studies have demonstrated that nitrogen can be fastened in an assimilable condition for crops via a distinct group of microorganisms, which are designated as biological nitrogen fixers (BNFs). These elements facilitate the colonization and nitrogen fixation of rhizosphere bacteria [5].

Nitrogen-fixing bacteria are non-symbiotic, free-living bacteria. They belongs to the family of *Azotobacteria* and are mainly used as a non-leguminous crop biofertilizer. The main nitrogen-fixing bacteria include symbiotic nitrogen-fixing bacteria, free-living nitrogen-fixing bacteria, and combined nitrogen-fixing bacteria, and the nitrogen-fixing bacteria associated with leguminous plants include *Rhizobium*, *Azotobacteria*, and slow-growing rhizobacteria [6][7], Associative nitrogen-fixing bacteria with nonleguminous plants encompass *Arthrobacter*, *Alcaligenes*, *Mycobacterium*, *Pseudomonas*, *Bacillus*, and *Azospirillum* [8]. Among them, *Rhizobium* represents the epitome of symbiotic nitrogen fixation and is one of the most comprehensive studies on the symbiotic relationship between root nodules and nitrogen-fixing bacteria [9]. *Rhizobium* perceives flavonoid compounds exuded from plant root systems to produce signals for reciprocal communication with the root microbiome [10]. For instance, secretions from peanut root can stimulate the rhizobium of peanuts. *Rhizobium* is attracted to the root's secretions, then forms nodules and fixes nitrogen in the roots of the host plant [11]. In addition, it was observed that the association of alfalfa with *Rhizobium* can enhance biological nitrogen fixation, stimulate plant growth, and more pertinently, rehabilitate heavily metal-contaminated soil while augmenting the resistance of plants to metals [12].

2.1.2. Phosphate Solubilizing

As an indispensable second nutrient element for plant growth and development, phosphorus contributes to important physiological processes such as plant metabolism, root growth and development, and flowering and fruiting [13]. Due to long-term application of chemical fertilizers, more than 70% of phosphorus in soil exists in inorganic form, and this inorganic phosphorus can easily react with Fe^{3+}, Al^{3+} and Ca^{2+} in soil to form insoluble phosphate [14]. Consequently, the addition of beneficial microorganisms is required to solubilize phosphates from the soil. It has been reported that species of bacteria and fungi, including *Bacillus*, *Rhizobium*, *Pseudomonas*, *Penicillium*, *Aspergillus*, and *Staphylococcus*, are typical phosphorus-enhancing agents [15]. The presence of insoluble phosphate in soil requires its conversion into soluble phosphate by soil microorganisms. Soil bacteria and fungi are involved in the solubilization process of soil phosphate by producing different mechanisms of action. Some of the mechanisms of action include the secretion of organic acids by beneficial bacteria, the formation of chelates, ion exchange reactions, etc. [16]. These beneficial microorganisms secrete organic acids that lower soil pH, thereby increasing the effectiveness of phosphorus in the soil [17]. Through these dissolved phosphorus microorganisms producing organic acids, secreted enzymes, iron carriers, etc., metal ions in the soil are chelated to form a complex, which is converted into phosphate, which can be absorbed and utilized by plants [18] [19]. They contribute to phosphate solubilization, increase phosphate utilization by the plant, and enhance physiological processes in the plant.

2.1.3. Potassium Dissolution

Potassium is the third most essential nutrient, following nitrogen and phosphorus. Potassium is abundant in soil and exists in various forms. It plays a pivotal role in a plant's growth and development, influencing plant growth, root system development, and enhancing yield and quality. The majority of potassium exists as in mineral form, which plants cannot directly assimilate. It has been documented that utilizing the distinct mechanisms of bacteria and fungi enables the transformation of insoluble potassium into soluble potassium. For instance, *Bacillus*, *Arthrobacter*, *Azotobacter*, and *Aspergillus* are archetypal potassium solubilizers. Research indicates that the *Bacillus and Klebsiella* isolated from the root zone of chili could solubilize substantial amounts of potassium in the soil, with the potential for potassium dissolution to exceed 70% compared to that of the control [20]. Recently, a study has indicated that the isolation of potassium-solubilizing bacteria from the rice rhizosphere enhances soil potassium availability and subsequently stimulates growth and yield in rice [21].

2.1.4. Regulating Phytohormone Levels

Additionally, phytohormones, also referred to as plant stimulators, are produced by PGPR and promote plant development [22]. The growth and development of crops are controlled by stimulating the plants. Microorganisms manufacture phytohormone, which are organic substances that regulate various aspects of plant growth, including cell division and differentiation, organ development, fruit ripening, flower blossoming, and fruiting. Auxins, cytokinins, gibberellins, ethylene, and abscisic acid are examples of phytohormones.

The widespread plant growth regulator auxin (also known as indole-3-acetic acid, indole-acetic acid, or IAA) is essential for promoting vegetative development [23]. The majority of PGPR generate indole acetic acid, which is essential for coordinating the host plant's and microbiota's interaction. In the rhizosphere, tryptophan (Trp), a substance found in root exudates, is exchanged between the plant-beneficial rhizobacterium and the host plant to facilitate communication [24]. As a signaling molecule that facilitates communication between Rhizobia and the host plant, tryptophan triggers PGPR to synthesize IAA through a variety of pathways [25]. IAA is an intrinsic regulator of plant development that mainly controls the growth of plant roots, promotes the creation of root hair, and stimulates the genesis of root epidermal cells. Furthermore, IAA influences photosynthesis, promotes plant cell differentiation and division, and aids in the creation of vascular bundles. One study used Helicobacter *Azotrophicus* inoculation to examine the impacts of root development in Arabidopsis thaliana in Brazil. The findings indicated that the growth hormone encouraged the production of lateral root meristematic tissues [26].

An essential plant hormone required for plant growth and development is cytokinin. It is primarily produced by inter-root bacteria, which use the synthesis of cytokinins to stimulate and support plant growth [27]. Plant growth and development activities, including root development and hair creation, stem and root elongation, light response regulation, and stomatal open-in promotion, are primarily driven by cytokinins. Furthermore, research has demonstrated that gibberellins (GA) are also produced by PGPR. Gibberellins primarily break dormancy in seeds and encourage germination; they also lengthen stems, induce the growth of floral organs, and increase fruit set. For example, gibberellin can protect the host plant against stress-related dangers when environmental conditions are unfavorable. Furthermore, certain species of inter-root bacteria release and manufacture ethylene, a special regulator of plant growth. They primarily control the growth and development of plants, encourage the growth of roots, and quicken the ripening of fruit. Ethylene's mode of action greatly increases plant vegetative growth and development, hastens plant maturity, which lowers plant consumption of soil nutrients, and increases the amount of soil nutrients that can be retained in the soil, minimizing the need for phosphorus and potassium fertilizers.

2.1.5. Iron Carrier Production

Iron is essential for the growth and metabolism of plants, primarily for the regulation of several physiological processes. For instance, respiration, photosynthesis, and nitrogen fixation all guarantee the availability of nutrients for plant growth. Because of its great susceptibility to oxidation, iron in soil can precipitate insoluble iron oxide, which plants cannot absorb [28]. The slow rate of decomposition of the majority of the inorganic iron minerals in rhizosphere soil inhibits the growth and development of plants. By employing a variety of mechanisms, PGPR can increase iron solubility by generating a number of tiny molecules known as iron carriers [29][30]. Low-molecular-weight, organic secondary metabolites generated by specific bacteria are called iron carriers [31]. These organic compounds are mostly used by microorganisms as iron chelators, helping them to absorb iron. These iron chelators can reduce the stress that heavy metals place on the environment by chelating iron as well as other heavy metals. Iron carrier complexes are created on the cell membrane by metabolites released by iron carriers interacting with Fe^{3+}. Eventually, these complexes are broken down to Fe^{2+}, which plants can absorb and use to support development. Numerous studies support the idea that *rhizobacteria* connected to plants that promote plant growth are also able to produce iron transporters. For example, by producing iron carriers and P solubilization, PGPR isolated from soil can improve the nutritional growth features of tomato plants, thus increasing nutrient efficacy [32]. Importantly, the *Burkholderia* P10 strain clarifies how the P10 transcriptome affects the transformation of peanut root exudates. Furthermore, it greatly amplifies the P10 strain's promotion of plant development by promoting the biosynthesis of iron carriers, the synthesis of IAA, and the expression of genes linked to phosphorus dissolution [33].

2.2. Increasing Crop Resistance to Environmental Stress

Reactive oxygen species (ROS) produced during environmental stress during plant growth impair plant productivity by causing organelle damage and eventual cell death [34]. Plants experience both biotic and abiotic stressors during their reproductive processes, leading to lower agricultural yields [35]. Fungi, bacteria, viruses, nematodes, and other biological creatures are all included in biotic stress [36]. Fungi, bacteria, viruses, nematodes, and other biological organisms are all included in biotic stress [37]. To maintain the agricultural ecological balance, according to the pressure encountered, researchers should implement effective solutions to the current environmental pressure and deal with the influence of various pressures [38]. As a result, some defense mechanisms are used to lessen the severe stresses that plants face [39]. On one hand, the genetic modification of crop varieties can foster robust crops that can withstand environmental fluctuations. However, it is crucial to consider that this process of nurturing resistant crop varieties is time-consuming and demands a considerably high investment in time. Currently, the principal methodology employed to alleviate plant environmental stress is the utilization of advantageous growth-promoting microbe of root zone soil [40]. PGPR impart antagonistic substances in the rhizosphere through suppressing pathogen growth and competing for nutrients [41]. PGPR mainly use various metabolites and volatiles to regulate the structure of soil microbial communities, suppress soil pathogens, and improve soil health. For example, PGPR produce antibiotics, hydrolyte enzymes, and antimicrobial compounds for use in attacking pathogen growth, thereby protecting plants from pathogens. PGPR improve plant growth and resistance through a number of mechanisms of action, providing effective alternatives to traditional control methods [42].

2.2.1. Biotic Stress

- Biological Control of Pest Management

Previously utilized pesticides and insecticides for biological control have a discernible negative impact on soil and human health. Some plant growth-inducing bacteria can protect plants from pests through pathogenic mechanisms, metabolites, and secretions. However, PGPR-based biocontrol agents are effective alternatives to synthetic pesticides and insecticides. For example, *Bacillus* and *Pseudomonas* are effective against pests [43]. *Bacillus thuringiensis* (Bt) is a prominent plant growth-promoting rhizobacterial biological insecticide, extensively applied to noctuidae, coleoptera, and diptera in insect classification [44]. *Bacillus thuringiensis* is a bactericidal protein and a quick-acting insecticide possessing minimal side effects on host plants and other beneficial micro-organisms [45]. It has been reported that *Bacillus* 90 and *Pseudomonas aeruginosa* strain 91k were evaluated in wheat studies and found to be effective against aphid populations [46]. PGPR secretion of volatile organic compounds helps defend against nematode damage and triggers ISR to resist pathogen attack [36]. It has been reported that the use of PGPR is effective in controlling potato nematode damage without secondary environmental pollution to the environment [47].

- Plant Pathogen Management

The defense mechanisms of PGPR protect against pathogenic bacteria, viruses, and fungi by inducing systemic resistance (ISR) and systemic acquired resistance (SAR) in plants [48][49]. PGPR-dominant strains that induce ISR include *Pseudomonas*, *Bacillus*, and *Serratia*. ISR is an activation response induced by a diverse array of beneficial and detrimental microorganisms, as well as environmental stressors. It is not possible to unequivocally discern the mechanism that induces ISR [49][50]. The primary mechanism by which PGPRs defend plants from biotic stress is their capacity to synthesize antibiotics [51]. Antibiotics are polyvalent microbe-derived substances of a low molecular weight possessing toxic organic components that can enhance plant growth and various metabolic activities [52]. Antibiotics are classified into two categories, namely volatile complex compounds and non-volatile complex compounds. Significantly, different types of beneficial bacterial genera in PGPR can produce antibiotics as a potent method to combat the invasion of pathogens. The dominant genus taxa producing antibiotics include *Pseudomonas fluorescens*, *Bacillus*, *Actinobacteria*, *Enterobacteriaceae*, and *Arthrobacter*. Antibiotics not only provide direct resistance to pathogens but also promote disease suppression in plant systems by inducing systemic resistance, conferring a competitive advantage to biocontrol agents. Nowadays, *Pseudomonas fluorescens* has the potential to protect against plant pathogen attacks as an effective control agent against plant pathogens [53]. *Bacillus* is a dominant genus within PGPR, efficiently combating plant pathogens. *Bacillus* also produces distinct antibiotic classes, primarily *Bacillomycin*, *Rhizobiumin*, and *Mycobacteriumin.* It is also known to generate antimicrobial surface-active agents [49]. In particular, *Bacillus* subtilis stops pathogens through biological control. In addition to this, *Bacillus* can produce iron carriers and extracellular polysaccharides to help regulate ionic balance and synthesize microbial metabolites to help control the threat of plant diseases. In addition, hydrolytic enzymes mainly include cellulases, proteases, chitinases, and lipases. Their main mechanism of action contributes to the hydrolysis of polymeric compounds, cleaving the cell walls, proteins, and DNA of pathogens to protect plants from pathogens. These volatile organic compounds can regulate the structure of soil microbial communities, in turn affecting the growth and development of fungi, plants, and animals. The accumulation of beneficial soil microorganisms can be stimulated via the application of biofertilizer with exogenous beneficial bacteria, in turn leading to the formation of beneficial flora against pathogens and ultimately to the recruitment of more disease-resistant microorganisms.

2.2.2. Abiotic Stress

- Drought Stress

Among abiotic stresses, drought is an important factor affecting agricultural production. Water scarcity affects plant physiological processes, water–nutrient relationships, and the normal metabolic activities of the plant body [54][55]. Currently, several strategies are necessary to overcome drought stress. The use of PGPR as inoculants alleviates water supply deficiencies and effectively promotes water utilization. The primary mechanism for the palliative effect of PGPR in drought is derived from the regulation of plant hormones, volatile compounds, and cell wall polysaccharides, which influence the normal growth of crops [56]. Through these mechanisms of action, they helps plants maintain survival under extreme drought conditions. The synthesis of phytohormones by *Pseudomonas*, *Bacillus* and *Rhizobium* isolated by PGPR is conducted to stimulate plant growth and overcome the stress of drought stress [57]. Under arid conditions, the introduction of beneficial microbial agents can generate extracellular polysaccharides (EPS), synthesize proline, and secrete phenolic compounds, and regulate plant growth and development to resist dehydration stress [58]. Salicylic acid (SA), primarily produced by microorganism-derived phenolic compounds, serves as a critical signaling molecule in arid conditions. It effectively activates antioxidant genes and underived metabolic gene products to manage plant growth and development [59]. ACC is a precursor of ethylene, and PGPR-produced ACC deaminase can degrade ACC levels, preventing an excessive increase in ethylene and thereby resisting abiotic stress [60]. It has been reported that PGPR strains produce 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase, which protects tomato from the negative effects of drought stress and significantly enhances the drought tolerance of plants [61]. Another study also reported that under drought and salt stress conditions, three beneficial PGPR isolates increased the IAA content, decreased the ABA/ACC content and improved the photosynthetic efficiency of wheat, thereby increasing its tolerance to abiotic stresses [62]. Research suggests that interspecific hybrid corn employs the PGPR-based isolation of *Pseudomonas putida*, *Pseudomonas fluorescens*, and *Bacillus megaterium* under conditions of drought stress. In the case of *Pseudomonas* putida treatment, seedling germination vitality, fresh and dry weight, dry matter content, and grain yield exhibit superior outcomes [63]. The inoculation of wheat in potting soil under drought conditions using two novel PGPR isolates, *Bacillus subtilis*-FAB1 and *Pseudomonas aeruginosa*-FAP3, stimulated plant growth and effective inter-root colonization, resulting in normal plant growth [64]. In recent years, the latest mechanisms of drought resistance have been mainly based on molecular and histological techniques to study some drought-resistant genes, contributing to researchers' understanding of the multiple functions of rhizobia under drought conditions. It was shown that, using a metabolomics approach with untargeted liquid chromatography using UHPLC, sorghum was inoculated with key molecules for PGPR-induced tolerance to drought stress in sorghum [65]. Similarly, the characterization of chickpea physiological and biochemical traits under drought conditions via 16S-rRNA gene sequencing and the identification of the dominant PGPR strains such as *Bacillus subtilis* and *Bacillus thuringiensis* led to changes in the metabolome to reduce the effects of stress [66].

- Salt Stress

In recent years, salt stress has become an important factor limiting plant growth. Excessive salinity leads to soil crusting, which further reduces the effective use of water by plants. Salinity directly affects the growth of the plant root system, which further impacts the entire growth process and metabolic activities of the plant [67]. Salinity directly affects chlorophyll content and carotenoids, denaturing the ultrastructure of the chloroplast, thereby reducing stomatal conductance and curtailing leaf photosynthesis. Increased levels of reactive oxygen species in plant cells are due to salt accumulation in the soil, leading to oxidative stress in plants [68]. Salinity can induce the accumulation of Na^+ and Cl^-, and at the same time impair the absorption of K^+ and Ca^{2+}, leading to an imbalance in ion homeostasis [69]. Consequently, it is necessary to employ strategic measures to mitigate the effects of salinity stress on plants. Extensive research indicates that PGPR can be leveraged to reduce crop yield losses resulting from salinity. PGPR influences plant physiological and biochemical processes through diverse mechanisms, mitigating the restrictions caused by salt stress on plant growth. Its primary mechanisms encompass the regulation of ion homeostasis, synthesis of protective agents against osmotic stress, activation of antioxidant enzymes, etc., all of which contribute to crop development [70]. Through the interplay of mechanisms and root zone microbiology, intricate signal networks regulate defensive mechanisms, alleviating stress [71]. It has been shown that inoculating rice seedlings with *Pseudomonas aeruginosa* and *Klebsiella* significantly increased plant height, root length, and plant dry weight, as well as promoting rice growth under salt stress conditions [72]. It has been reported that using *Bacillus* to investigate the growth of tomatoes under salt stress was found to induce systemic tolerance in tomato plants and had a significant impact on the diversity of the bacterial community [73]. It has also been reported that the beneficial *Bacillus* sphaericus SQR9 secretes spermidine, which induces salt tolerance in Arabidopsis thaliana and maize, enhancing their salt tolerance [74]. Therefore, PGPR can effectively resist the negative effects of salt stress, improve the salt tolerance of plants, and induce the development of resistance systems in plants.

- Heavy Metal Stress

In addition to drought and salt stress, heavy metal pollution also has a negative impact on sustainable agricultural development. Due to increased heavy metal concentrations attributed to various anthropogenic activities, soil health has been compromised, directly influencing plant enzyme activity and nutrient transformation. Consequently, plant growth and development are hindered [75]. Thus, it is imperative to implement certain strategies to remediate contaminated soil. The utilization of microorganisms, specifically PGPR, in support of bioremediation technology has garnered widespread attention [76]. The primary objective of the microbiological remediation of soil heavy metals is to first immobilize the heavy metal, subsequently reduce its mobility, and ultimately remove it from the soil. The primary heavy metals include manganese, cadmium, iron, and zinc; the majority of microorganisms can absorb soil heavy metals through various mechanisms. The deposition in the affected soil exerts a detrimental effect on plant growth, root system development, photochemical properties, and nutrient assimilation [77]. The mechanism predominantly involves the binding of certain surface heavy metals by live microbial cells and surface-active substances. Concurrently, microorganisms undergo growth and metabolic processes that generate certain inorganic salts and hydrogen peroxide metabolites. These substances react with heavy metal ions to form precipitates [78][79]. In heavy metal-contaminated environments, microorganisms produce iron carrier chelators that can bind to various heavy metals, reducing their toxicity and promoting the growth of barley [80]. In a study on spinach, *Bacillus subtilis* and *Pseudomonas aeruginosa* were inoculated to enhance transpiration rate, stomatal conductance, and relative water content, as well as to improve resistance to heavy metal stress. This process also increased the capabilities of the antioxidant defense system [81].

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