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*Review*

# Exopolysaccharide-Producing PGPR: Mechanisms for Alleviating Salinity-Induced Plant Stress

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## Abstract

Elevated salinity levels pose a significant challenge to global crop production, affecting approximately 85% of the Earth's arable land. The stress induces disruptions in vegetative development and yield by inducing osmotic imbalance, toxicity from ions, and membrane instabilities, ensuing in a substantial fall in crop production. However, the administration of EPS-producing bacteria promises an optimistic approach that can minimize the effects of salinity and boost crop resistance in saline conditions. EPS-producing bacteria have a dynamic role in reducing the harmful effects of salt stress through several mechanisms, such as restricting the absorption of sodium, improving the intake of beneficial ions such as $K^+$, $Ca^{2+}$, $Mg^{2+}$, and P, elevating levels of antioxidants, and encouraging the establishment of soil aggregates. These bacteria assist in regulating ion balance in plant cells experiencing salt stress, hence improving plant development traits and stress tolerance. When the level of salt elevates in the soil, these bacterial strains form a protective layer (biofilm) around roots and prevent the uptake of sodium ions into the plant. EPS also forms complexes with sodium ions in the soil, so decreasing their accessibility for plant uptake and contributing to the maintenance of an ideal ion equilibrium for plant survival. In addition, bacteria that produce EPS enhance soil structure and fertility by promoting soil aggregation, enhancing nutrient availability, and improving water retention capacity. EPS-producing bacteria have a crucial role in enhancing the health and productivity of plants cultivated in saline environments. In addition, bacteria that produce EPS show positive impacts on the efficiency of photosynthesis, the amount of water in plants, and markers of oxidative stress in plants that are exposed to salt stress. These bacteria improve photosynthetic rates by enhancing food availability and water uptake in the rhizosphere, resulting in higher chlorophyll production and overall plant development. Furthermore, bacteria that produce EPS increase the water content in plant tissues, resulting in better hydration and overall plant health. Furthermore, these bacteria reduce levels of oxidative stress markers such as malondialdehyde (MDA) and hydrogen peroxide ($H_2O_2$), therefore increasing antioxidant defenses and reducing oxidative damage in plants subjected to salt stress.

**Keywords:** PGPB, salinity, abiotic stress, plant growth promotion, soil aggregation, environmental sustainability

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## Introduction

Abiotic stressors that harm a plant's physiology, metabolism, and growth attributes, such as salt, heat, cold, drought, and heavy metals, are significant barriers to agricultural productivity [1]. Many times, plants are exposed to a variety of challenges, which are made worse by environmental pollution, chemical fertilizers, pesticides, and climate change [2]. With the world population predicted to expand by approximately 10 billion by 2050, this scenario is projected to become much more concerning [3, 4]. To meet the need, food production must immediately rise by 70% [5]. Finding ways to put novel agricultural strategies into practice is also essential for shielding crops from these numerous abiotic stresses [6-8].

Due to abiotic stressors, agricultural systems are significantly impacted by oxidative stress, which can have a detrimental effect on plant strength, productivity, and crop yield as a whole. Oxidative stress arises from an imbalance between the generation of reactive oxygen species (ROS) and the plant's antioxidant enzymes, leading to harm to cells and disruptions in physiological processes [9, 10]. Various elements, such as bright sunlight, dryness, salt, high temperatures, pollutants, and microbial diseases, have been scientifically demonstrated to induce oxidative damage in agricultural activities [11, 12]. Stressors can lead to an overproduction of hydroxyl radicals (•OH), superoxide radicals ($O_2^-$), and hydrogen peroxide ($H_2O_2$). These extremely reactive compounds have the potential to induce oxidative harm to biological constituents such as proteins, lipids, and genetic material (DNA) [13]. It results in lower biomass accumulation, which eventually leads to decreased reproductive success and compromised seed germination. Oxidative stress also has a detrimental impact on crop production and quality [14]. Furthermore, oxidative stress impairs a plant's defense against pathogen invasions, leaving crops more vulnerable to disease [15].

Reactive oxygen species (ROS) are commonly generated in plant tissue due to stress, which leads to oxidative stress. Oxidative stress is defined as the disruption of the equilibrium between oxidation and reduction processes within a cell due to a higher level of reactive oxygen species (ROS). Nevertheless, a contemporary conceptualization of oxidative stress posits that it encompasses a state of imbalance between oxidants and antioxidants, wherein oxidants surpass antioxidants in significance. The aforementioned disparity may lead to the disturbance of redox signaling and regulation, along with molecular harm [16]. In contemporary times, the classification of oxidative stress has been divided into two distinct subtypes: eustress, denoting oxidative stress that arises spontaneously within physiological contexts, and distress, denoting oxidative stress that induces detrimental effects on macromolecules [17].

Although oxygen is essential for energy metabolism and breathing, it is paradoxically linked to the beginning of different illnesses and aging processes [18]. Over a span of two billion years, the oxygen levels on Earth experienced a significant rise due to the emergence of photosynthesis, first by blue-green algae and then by plants. The production of molecular oxygen in this natural process is a secondary result facilitated by the oxygen-evolving complex (OEC), which is an element that makes up the photosystem (PS) II [19]. The presence of a large quantity of oxygen enabled the production of a greater amount of ATP via aerobic respiration while concurrently increasing the likelihood of reactive oxygen species (ROS) formation. According to Dumont and Rivoal [20], aerobic organisms exhibit antioxidant defense systems that facilitate their survival and protection against various reactive oxygen species (ROS).

It is also found that molecular oxygen possesses the capacity to act as an oxidant [21]. Nevertheless, despite the notable thermodynamic reactivity exhibited by molecular oxygen, its reactions are distinguished by sluggish kinetics owing to the existence of spin restriction. Oxygen, in its lowest energy form, is found in $^3O_2$ (as a triplet), having two electrons that are not in two different orbitals, each with an opposing spin. This configuration results in the paramagnetic nature of oxygen, wherein it lacks any inherent attraction towards organic molecules unless it undergoes activation [22, 23].

Plants have a sophisticated antioxidant system of defenses comprising antioxidants, which may be enzymatic and non-enzymatic, which aids in mitigating the detrimental impacts of oxidative stress. Enzymes, including SOD, POD, CAT, and glutathione reductase, are types of enzymatic antioxidants that remove and neutralize reactive oxygen species (ROS). [5, 24]. Ascorbate (vitamin C), glutathione, carotenoids, and tocopherols are examples of non-enzymatic antioxidants that are important in ROS detoxification [25, 26]. It is crucial to comprehend the significance of oxidative stress in agricultural systems in order to create efficient plans to increase crop resilience and output. Researchers are concentrating on a number of methods to reduce oxidative stress, such as selecting crop varieties that are resistant to stress, enhancing cultural practices, and applying exogenous antioxidants [27, 28]. In addition, recent research investigations have demonstrated that using helpful microbes, such as rhizobacteria and mycorrhizal fungi, might reduce oxidative stress in agricultural systems [29-31]. These bacterial and fungal strains can boost plants' antioxidant defenses, control ROS generation, and encourage nutrient uptake, all of which help plants tolerate oxidative stress better, as shown in Fig. 1.

Different biochemical substances are produced by PGPB, which helps alleviate salinity stress. Exopolysaccharides (EPS) play a crucial role in safeguarding plants against salt stress, particularly

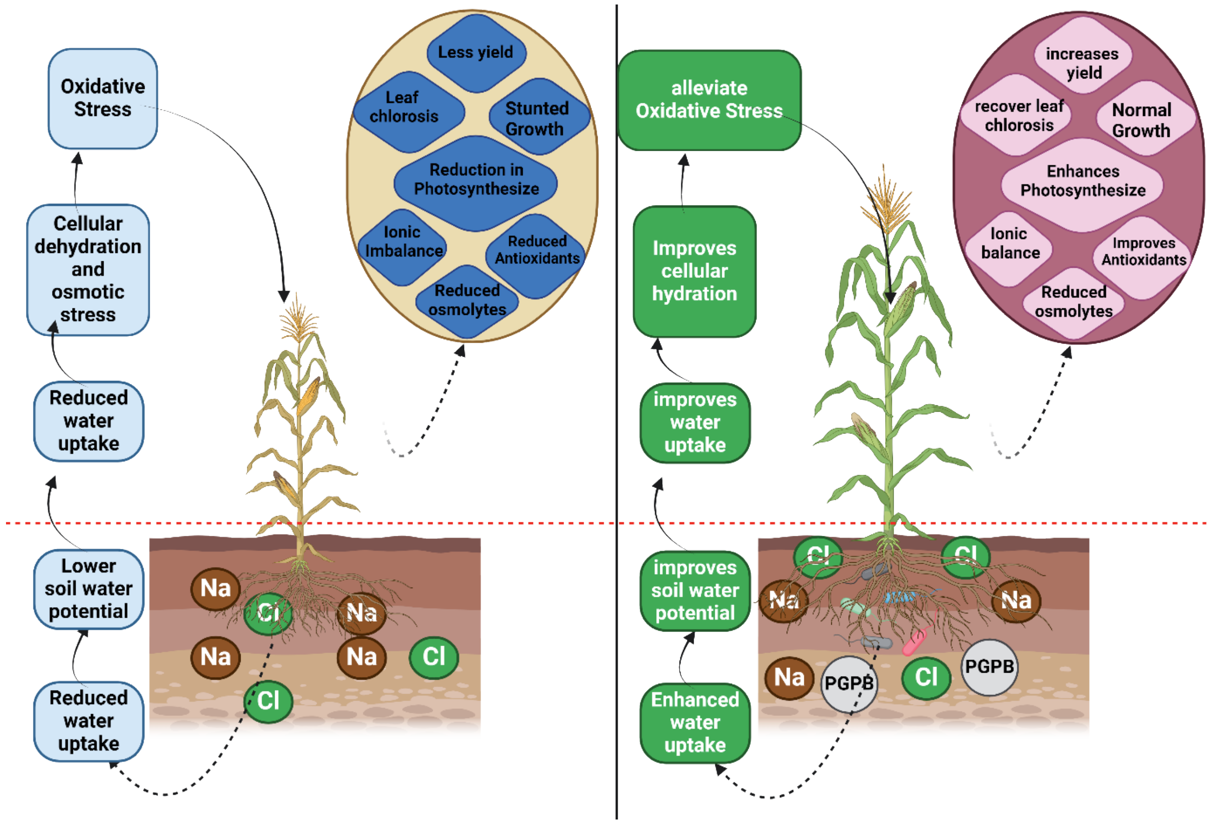


Fig. 1. The negative impacts on different morphological and biochemical attributes of salinity stress on plants and the role of exopolysaccharides (EPS) producing PGPB to alleviate the negative effects.

when produced by halotolerant plant growth-promoting bacteria (PGPB) [32]. Polysaccharides produced by bacteria in the surrounding environment form a protective biofilm around plant roots, reducing direct exposure to high salt concentrations [33]. This biofilm retains moisture in the root zone, enhances osmotic balance by improving water availability, and sequesters toxic ions, including sodium (Na) and chloride (Cl), thereby reducing ion toxicity [34]. EPS improves soil aggregation, which enhances soil structure, aeration, and root penetration. This enhancement reduces the negative impacts of elevated salinity on root development and nutrient uptake. EPS may alter plant responses to stress, potentially enhancing the production of antioxidants and osmoprotectants, thereby improving stress resilience in plants [5].

This method innovatively incorporates natural microbial processes to enhance plant resilience under salinity stress [35]. EPS concurrently tackles various challenges, such as osmotic adjustment, ion sequestration, and enhancement of soil structure, instead of focusing on a single target. Extracellular polymeric substances (EPS) form a biofilm around roots, establishing a physical barrier that protects roots from direct salt exposure, thus improving root health and function. This method promotes sustainable agriculture by enhancing soil health via improved soil aggregation and nutrient cycling rather than relying on chemical amendments [36]. This method employs halotolerant bacteria and their capacity to produce extracellular polymeric substances (EPS). This approach is a comprehensive, bio-based, and eco-friendly method to enhance plant growth and resilience under saline stress, serving as an alternative to conventional techniques [37-39].

## The Importance of PGPB in Reducing Oxidative Stress

A class of bacteria known as plant growth-promoting rhizobacteria (PGPR) live in the root zone or rhizosphere and enhance crop growth. They contribute to improving crop production [40]. According to Singh et al. [37], certain genera in the microbial community, such as *Bacillus, Cronobacter, Enterobacter, Bacillus, Pseudomonas*, *Kocuria*, *Azotobacter*, and others, are well known for their services in oxidative stress alleviation. According to different studies [41-43], these bacteria are essential for enhancing plant growth through facilitating nutrient transportation, releasing plant hormones, and maintaining a harmonious equilibrium of nutrients and hormones. PGPR can be categorized into two primary classifications: Mutually beneficial (symbiotic) and free-living rhizobacteria are two distinct types of bacteria that reside in the rhizosphere, which refers to the region of soil that surrounds the roots of plants [44].

Mutually beneficial rhizobacteria are microbes that form a mutually advantageous association with agricultural crops, positively affecting their development through lowering stress and offering biofertilization. Still, free-living rhizobacteria in the ground have the ability to establish colonies, impact accessibility to nutrients, and ensure disease resistance in plants [45].

Plant growth-promoting rhizobacteria (PGPRs) have attracted considerable attention in the field of plant science due to their remarkable research achievements. Table 1 displays a collection of data that provides evidence to support this assertion. Furthermore, the inherent metabolic and genotypic capabilities of these organisms to resist unfavorable situations have made them the most significant factors in developing tolerance to abiotic pressures [46]. However, the mechanism by which PGPR enhances resilience to stress involves a combination of direct and indirect actions.

The latest research demonstrates that direct techniques involve stimulating the development of plants by excessive production of phytohormones and improved uptake of nutrients and water, as well as associated activities. Conversely, indirect approaches mainly comprise antagonism, the production of hydrolysis enzymes, and the release of the right solutes [47]. Moreover, research has shown that PGPR has the ability to produce certain factors, such as sigma, which have an important role in regulating the expression of genes and helping to mitigate the negative impacts of environmental stimuli [48].

## Introduction to Exopolysaccharide-producing Bacteria

Exopolysaccharides (EPS), which are generated and released by specific bacteria, are complex polymers made up of sugar units. These microbial EPS have drawn a lot of attention across a range of disciplines because of their unique features and possible uses [49, 50]. Microbes that produce exopolysaccharides come from a variety of taxonomic families, including bacteria, archaea, fungi, and algae. They have the ability to create and release EPS into the environment. The complex process of producing EPS is regulated by a number of variables, including nutrition availability, ambient conditions, and microbial physiology [51]. ESPs consist of a diverse combination of biomolecules that form a three-dimensional structural matrix. The matrix consists of enzymes, polysaccharides, structural proteins, sugars, extracellular DNA, nucleic acids, amino sugars, lipids, pyruvates, humic compounds, and glycoproteins [35]. The physicochemical qualities and functions of each of these components exhibit variation. EPS commonly contains extracellular carbohydrate substituents such as pyruvates, acetate esters, succinates, and formates [52] Fig. 4. The EPS structure consists of recurring monosaccharide units, which can be categorized as either homopolysaccharides or heteropolysaccharides [53].

Homopolymers consist of individual sugars, including pentoses (such as xylose and arabinose), hexoses (such as allose, glucose, mannose, and galactose), desoxyhexoses (such as fucose and rhamnose), amino sugars (such as glucosamine and galactosamine), and uronic acids (such as galacturonic acids and glucuronic acids). The sugars are joined together by strong 1,4-β- or 1,3-β-l bonds, as well as more flexible 1,2-α- or 1,6-κ- bonds. Heteropolysaccharides are composed of up to three distinct sugar molecules that are arranged in a repetitive manner. Cations can form associations with proteins and lipids to form glycoproteins and glycolipids, respectively. Similarly, they associate with acids such as galacturonic acid, glucuronic acid, and mannuronic acid, or may also associate with extracellular DNA. Uronic acids, phosphate and sulfate residues, succinate and pyruvate substituents, and uronic acids all contribute to the matrix's negative charge. This negative charge helps in the absorption of different cations like metals, sodium, and potassium, as shown in Fig. 2 [33].

The enhancement of soil quality and fertility can be achieved by employing microbial-extracted plant products (EPSs) [54, 55]. Because of their large molecular mass, extracellular polymeric substances (EPS) are essential for both improving soil particle preservation and soil microbe adhesion to the outside of the particle. A variety of processes, including bonding with hydrogen, cationic bonding, anion adhesion, and van der Waal's interactions, allow EPSs to adhere to soil surfaces [56]. The aforementioned organic result has the ability to improve the solidity of soil aggregate aeration, permeability, and root penetration, as well as decrease drainage by reducing moisture and swelling. EPS contributes to the process of soil micro aggregation by the formation of an organo-mineral sheath. The application of this coating enhances the structural integrity of the soil and enhances its stability when subjected to stressful situations [57]. Table 1 displays a comprehensive compilation of rhizosphere bacteria that exert a substantial influence on the growth of plants. The presence of these bacteria is crucial in regulating the interactions between plants and water, preserving ion equilibrium, and increasing the performance of plants in photosynthesis during drought and salt stress. The complex signaling network that facilitates stress reduction is facilitated by the interaction between plants and microbes [58]. EPS, or extracellular polymeric substances, are essential for preserving plant health in the face of abiotic stress. They serve as a nutritional facilitator and sticky matrix, enabling the attachment of bacteria to plants. A positive correlation exists between the production of extracellular polymeric substances (EPS) by bacterial cells and the presence of abiotic stress [59].

These microorganisms create EPS with a variety of chemical configurations, each of which confers special physical and biological features. These characteristics make EPS appropriate for a variety of uses in the food, pharmaceutical, agricultural, and

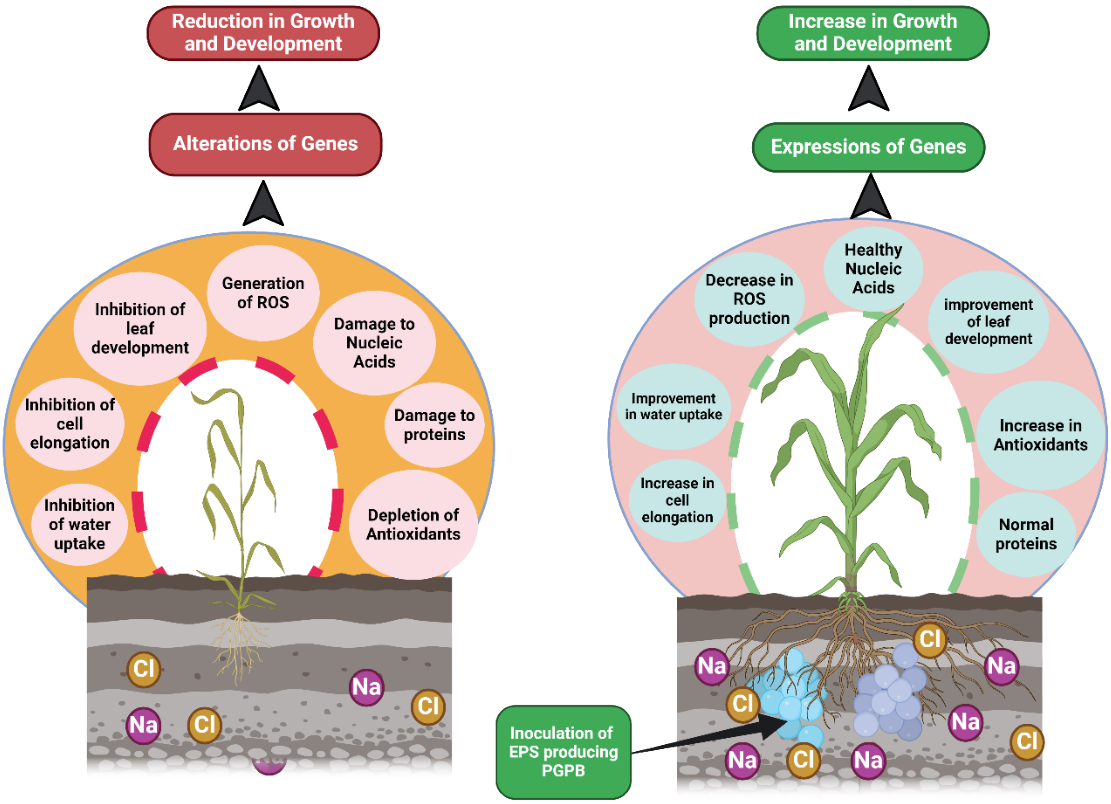


Fig. 2. Salinity stress leads to osmotic stress in plants. The application of EPS-producing PGPB alleviates the detrimental impacts of such stress on plants.

environmental engineering industries [60]. The genus Xanthomonas is one example of bacteria that produces exopolysaccharides. A well-researched bacterium called Xanthomonas campestris is well-known for its capacity to create xanthan gum, a crucial EPS for industry. The excellent thickening, stabilizing, and gelling qualities of xanthan gum make it useful in the food and beverage sector [61].

Table 1. EPS-producing bacterial strains alleviate salinity stress in different plants.

| Bacterial strain | Plant | Mechanism | Reference |
|---|---|---|---|
| *Alcaligenes* sp *AF7* | Rice | Increase in plant growth attributes and enhanced uptake of metabolites | [89] |
| *Azotobacter chrococcum C5* | Maize | The $K^+/Na^+$ ratio was raised, resulting in enhanced uptake of ions such as sodium, potassium, calcium, and magnesium dioxide. Additionally, there was an increase in the amount of chlorophyll, as well as the buildup of proline and polyphenols. | [86] |
| *Azotobacter chroococcum* | Faba Bean | Increased concentrations of nitrogen (N), phosphorus (P), and potassium (K); the content of proline; relative water content (RWC) percentage; and the ratio of potassium (K) to sodium (Na+); however, the concentrations of sodium (Na+) and chloride (Cl−) | [90] |
| *Bacillus insolitus, Aeromonas hydrophila,* and *Bacillus* sp. | Wheat | Stimulated the absorption of sodium, calcium, and potassium ions from salts, leading to improved production, as determined by measuring the dry weight of plants. | [91] |
| *Bacillus methylotrophicus* PM19 | Wheat | The presence of EPS has a beneficial impact on wheat seedlings germination, as well as on the length of their roots and shoots and the levels of photosynthetic pigments they produce. Additionally, contributed to the sequestration of sodium. | [32] |
| *Bacillus pumilus* | Wheat | Alleviate salt stress by decreasing the concentration of sodium that is accessible for plant absorption. | [88] |

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| *Bacillus pumilus strain FAB10* | Wheat | The topics of interest are photosynthesis, transpiration, and proline content in plant tissue. | [92] |
| *Bacillus pumilus strain JPVS11* | Rice | Enhanced plant growth characteristics, heightened levels of antioxidants, and increased amounts of photosynthetic pigments. Additionally, enhanced the absorption of nutrients. | [93] |
| *Bacillus* sp. | Lettuce | There is a gradual rise in the levels of minerals while the amounts of chlorine and sodium drop. | [94] |
| *Bacillus subtilis ESM14,* and *P. putida ESM17* | Tomato | Improved morphological parameters, RWC, antioxidants, and reduced uptake of Na+. | [95] |
| *Bacillus subtilis susp. Inaquosorum* and *Marinobacter lipolyticus SM19* | Wheat | Inhibited the absorption of sodium ions and promoted the absorption of potassium ions, resulting in an overall increase in biomass. | [96] |
| *Bacillus tequilensis* and *Bacillus aryabhattai* | Rice | The plant experiences an augmentation in photosynthesis, transpiration, and stomatal conductance, resulting in an elevated yield. | [97] |
| *Bacillus tequilensis UPMRB9* | Rice | Improved growth characteristics such as increased fresh and dry weight, and levels of antioxidants. Enhanced the absorption of nitrogen, phosphorus, and potassium while restricting the absorption of sodium ions. | [98] |
| *Burkholderia cepacia* | Wheat | Increased chlorophyll levels and enhanced plant development | [99] |
| *Burkholderia pyrrocinia* | Peanut | Enhanced the plant's fresh weight and root length by 90.12% and 79.22%, respectively. | [100] |
| *Enterobacter cloacae* and *Bacillus drentensis* | Mung bean | The production of biofilm in the root zone improves nutrient availability and water uptake in plants. | [101] |
| *Gluconacetobacter diazotrophicus* | Rice | Preserved plants against oxidative harm in laboratory conditions and when establishing in rice plants by restricting the absorption of Na and Cl. | [102] |
| *Glutamicibacter halophytocola KLBMP 5180* | Wheat | The crops can benefit from the antioxidant activity to reduce the damage caused by salt stress. | [103] |
| *Glutamicibacter* sp. *MK847981 and Pseudomonas* sp. *MK087034* | *Suaeda fruticose* | The concentration of Na+ decreased while the concentration of K+ increased, resulting in an increase in the K+/Na+ ratio. | [104] |
| Halomonas variabilis (HT1) and Planococcus rifietoensis (RT4) | Chickpea | Enhanced plant growth under high salt conditions. Furthermore, it led to enhanced soil aggregation and enhanced uptake of nutrients. | [105] |
| *Halomonas* sp. *EX01* | Rice | The process involves the promotion of soil aggregation and the enhancement of root adhering of soil (RAS) through the creation of a protective covering over the roots of plants. This leads to better absorption of nutrients from the soil, including potassium (K), phosphorus (P), nitrogen (N), and iron (Fe). It also increases the availability of water. | [106] |
| *Halomonas* sp. *Exo1* | Rice | Increased plant growth characteristics and raised levels of antioxidants | [12] |
| *Idiomarina zobelli* FMH6v, *Nesterenkonia halotolerans* FMH10 | Tomatoes | Enhanced plant development through the production of surfactants and restriction of Na+ absorption. | [107] |
| *Jeotgalicoccus huakuii NBRI 13E* | maize, tomato, and okra | Regulation of chlorophyll, defense enzymes, soluble sugar levels, and proline. | [108] |
| *Klebsiella variicola* SURYA6 | Wheat and maize | Increased absorption of nutrients and improved growth characteristics of plants. | [109] |
| *Kocuria rhizophila 14asp* | Pea | Increased growth characteristics and levels of chlorophyll. Furthermore, there is a notable rise in antioxidants. | [5] |
| *Pantoea alhagi* NX-11 | Rice | Enhanced growth via increasing the production and activity of proline synthase, decreasing the production of proline dehydrogenase, and boosting the activities of antioxidant enzymes | [110] |
| *Pantoea alhagi* NX-11 | Rice | Enhanced antioxidant activity leads to improved development. | [110] |

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| *Pseudomonas putida* | Sunflower | Plant hormones can promote tolerance to various abiotic stimuli, such as salt stress, and can contribute to soil aggregation. | [82] |
| *Pseudomonas putida RT12* | Mustard | Improved growth metrics and increased levels of antioxidants lead to a decrease in markers of oxidative stress. | [111] |
| *Pseudomonas simiae* | Soybean | Transcription of salt-resistant genes in soybean plants under saline regime. | [112] |
| *Pseudomonas simiae* MHR6 | Maize | Enhanced maize development in terms of seedling growth performance, antioxidant concentrations, chlorophyll levels, and osmotic regulation. | [113] |
| *Pseudomonas* sp. | Sunflower | Enhanced plant development by restricting sodium intake and promoting the activity of antioxidant enzymes. | [38] |
| *Thalassobacillus denorans* and *Oceanobacillus kapialis* | Rice | Enhances seed germination and enhances the absorption of nutrients, leading to increased plant vigor, chlorophyll levels, and biomass production. | [85] |

## Results and Discussion

### EPS-producing Bacteria's Role in Salt Stress Alleviation

Salinity stress greatly impedes plant development and productivity by causing osmotic stress, membrane instability, and nutritional imbalances. Consequently, the proliferation and maturation of plants are constrained. As per the Food and Agriculture Organization (FAO) of the United Nations [62], approximately 85% of the surface area of agricultural land has been shown to be affected by salinization. Increased amounts of salinity possess the capacity to elicit water lodging, which leads to ion toxicity, ionic imbalance, or a variety of both [63]. The existence of salinity poses a significant constraint on crop production, leading to a substantial decrease in yield of approximately 65% [64].

Beneficial bacteria play a crucial role in promoting plant growth by producing important substances called secondary metabolites. These include phytohormones, ACC deaminase, siderophores, volatile organic chemicals, and extracellular polymeric polymers [65]. Certain species of bacteria exhibit halotolerance, which is the capacity to withstand and thrive in saltwater environments due to their intricate biochemical and physiological mechanisms [66]. Genetic engineering is an innovative method that has the potential to create cultivars that can tolerate high levels of salt. However, this process is both expensive and time-consuming. The utilization of microbial technologies in agriculture is widely acknowledged as an essential approach for achieving long-term crop productivity [67]. Hence, the application of advantageous microorganisms to enhance the resilience of crops against non-living factors has emerged as a feasible and environmentally sustainable substitute [68, 69].

Ensuring ion homeostasis is essential in plant cells experiencing salt stress. The imbalance of other essential ions, such as potassium, in the cell is disrupted by an elevated absorption of sodium ions ($Na^+$) and chloride ions ($Cl^-$) [70]. Microorganisms emit a variety of organic and inorganic compounds, such as EPS, in natural environments or when triggered by exposure to unfavorable environments. The aforementioned process leads to the formation of a biofilm, where bacterial cells gather together and have the ability to adhere to different surfaces and absorb substances [71].

High molecular weight extracellular polymeric substances (EPS) have a crucial role in promoting cellular connections and communication. Observations have shown that the existence of versatile beneficial bacteria that may produce extracellular polymeric substances (EPS) improves the structure of soil by facilitating the production of crumbs, increasing the volume of large pores, and aggregating soil in the rhizosphere, as shown in Table 1. The aforementioned processes ultimately lead to an increase in water retention and improved nutrient accessibility for plants [62]. When faced with environmental stressors, strains that can tolerate salty conditions have the ability to produce EPS in different formulations and quantities. This, in turn, improves germination and leads to higher crop yields [72].

EPS serves as a physical barrier in soils with elevated saline levels, safeguarding roots and facilitating plant growth (Fig. 3). Recent research has revealed that bacteria in soil with high levels of salt are able to produce EPS, which improves the physical and chemical characteristics of the soil and encourages the creation of soil aggregates [59]. Microbes, such as bacteria, have the potential to make plants tolerant to salinity and stimulate growth in saline soil through a variety of mechanisms [18]. High soil salinity is lessened by the link that EPS makes with sodium ions, as shown in different studies in Table 1. Additionally, by controlling the balance of $Na^+$ and $K^+$ ions, which is essential for plant viability in unfavorable soil conditions, EPS produced by microbes helps to mitigate salt stress [5]. Plants that were injected with salt-tolerant bacteria that produce EPS were able to absorb more potassium, calcium, and sodium ions from the soil [28]. In the region of the roots, EPS and sodium ions combine to create a chelate, which effectively prevents the roots from moving to the stem and lowers the amount of sodium that is absorbed from the soil [70]. Elevated salinity levels stimulate the production of extracellular polymeric substances (EPS), which ultimately results in the development of biofilms [73]. Consequently, this improves sodium ion ($Na^+$) chelation. The composition of EPS is also influenced by the amount of NaCl present in the soil, observed an increase in trehalose and rhamnose. These saccharides act as a carbon source and encourage water retention, which helps bacteria deal with salt stress (Fig. 3). Research has indicated that the development of biofilms and the production of extracellular polymeric substances (EPS) provide several advantages for plants grown in highly salinized environments. By enhancing the survival rate of cells in the rhizosphere, they can enhance the fertility of the soil and promote plant development [74]. Microbes have a multitude of functions in plants, including defense against environmental stressors, surface area augmentation for adhesion, high population densities, enhanced plant tolerance to antibiotic treatments, and encouragement of plant-to-plant competition for nutrients [75]. Microbial organisms employ many tactics to mitigate the impact of salt stress, such as ion transport, osmotic balance, and induction of defense systems against oxidative stress [76]. Moreover, ACC deaminase, siderophores, and exopolysaccharides are just a few of the biochemicals that microbes can manufacture[77].

## Exopolysaccharide as a Tool for Halotolerance

Biofilm formation and the production of exopolysaccharides are two crucial mechanisms that enhance the ability of halotolerant or halophilic bacteria to withstand salt stress [78]. Rhizobacteria that promote plant growth have been identified as a potentially efficacious biological approach for mitigating salt stress in plants. Induced systemic tolerance (IST) allows bacteria to develop resistance to different abiotic stress situations, such as salt. Plant rhizobacteria that promote growth (PGPRs) cause noteworthy physiological and chemical changes that improve a plant's ability to modify its response to several non-living stimuli (Table 1).

Plants gain assistance in defending themselves against pathogens through the generation of siderophores, which help with the absorption of nutrients by synthesizing auxin, cytokinin, and gibberellin-like phytohormones. Moreover, they have a role in controlling ethylene levels in plants by acting as ACC deaminase [79]. In times of stress, the plant hormone ethylene assumes a pivotal function in upholding cellular homeostasis, resulting in a reduction in the growth of both shoots and roots. PGPR strains are capable of synthesizing exopolysaccharides (EPSs) which have the ability to adhere to soil particles, resulting in the formation of large and tiny aggregates. The capacity of plant roots to efficiently occupy the interstitial spaces among microaggregates plays a significant role in the stabilization of macroaggregates. Sandhya et al. [36] research has revealed that plants exposed to EPS exhibit heightened resilience to water and salinity stress, as well as improved soil structure. Acidic extracellular polymeric substances (EPSs) bind to sodium ions in a saline environment, rendering the salts inaccessible to plants. According to Shrivastava and Kumar [80], this procedure enables the reinstatement of plant development. The formation of acidic extracellular polymeric substances (EPSs) of the succinoglycan type has been primarily described in rhizospheric bacteria and plant growth-promoting rhizobacteria (PGPRs). Succinoglycan has the potential to improve the formation of nodules in leguminous plants grown in salty soils, which is in line with sustainable agriculture practices [81]. The results of a research study conducted on rhizospheric bacteria, namely *Aeromonas hydrophila, Bacillus insolitus*, and *Bacillus* sp., collected from salty soils, demonstrate a notable increase in the dry and fresh matter of both root and shoots in wheat seedlings when exposed to salt stress.

EPS producing microbe's role in terms of providing services to plants can be further divided into the following.

### *Role in Improving Growth Attributes*

The investigation of bacterial strains for their services in enhancing plant growth in salt environments has resulted in a wide range of discoveries, demonstrating the various ways in which these microbes interact with plants to improve their ability to withstand salinity stress. Two interesting candidates for wheat cultivation have been identified: *Bacillus subtilis* susp. *Inaquosorum* and *Marinobacter lipolyticus* SM19. Talebi Atouei et al. (2019) showed that their method effectively decreased the uptake of Na+ ions while concurrently enhancing the uptake of $K^+$ ions, leading to an overall rise in biomass. *Pseudomonas simiae* MHR6 has demonstrated significant efficacy in promoting maize growth parameters, as indicated by enhancements in seedling performance, antioxidant levels, chlorophyll content, and osmotic regulation (Liu et al., 2022). *Bacillus subtilis* ESM14 and *Pseudomonas putida* ESM17 have gained recognition in the field of tomato cultivation due to their capacity to enhance morphological characteristics, relative water content (RWC), antioxidants, and reduce $Na^+$ uptake (Haque et al., 2022). In addition, the bacterium *Bacillus methylotrophicus* PM19 has been shown to have a beneficial effect on the germination of wheat seedlings, in addition to their generation of photosynthetic pigments, sodium ion elimination, and the length of their roots and shoots. These findings highlight the potential of *Bacillus methylotrophicus* PM19 as a growth-promoting agent in environments with high salt levels. These studies highlight the various tactics used by bacteria to improve plant growth and reduce the negative effects of salt stress. *Azotobacter chroococcum* has become a substantial factor in enhancing the development of the *Faba bean* in the field of legume farming. Abd El-Ghany and Attia (2020) found that this bacterium has the ability to improve nutrient concentrations, relative water content (RWC), proline content, and the $K^+/Na^+$ ratio. This suggests that it can help reduce the negative impact of salinity stress on legume crops. *Enterobacter cloacae* and *Bacillus drentensis* have been found to improve the accessibility of nutrients to the plant and the absorption of water in mung bean plants by creating biofilms in the root area (Mahmoud et al., 2020).

Furthermore, much research has been conducted to examine the efficacy of microbe isolates to boost rice growth. The research work of Sun et al. (2020) shows that *Pantoea alhagi* NX-11 improves rice development by increasing the concentrations of proline synthase, decreasing proline dehydrogenase, and raising the activities of antioxidant enzymes (Table 1). Furthermore, research has demonstrated that *Gluconacetobacter diazotrophicus* has the ability to safeguard rice plants against oxidative harm and restrict the uptake of sodium and chloride ions, respectively, when colonizing, thereby improving plant growth in saline environments (Meneses et al., 2017). Furthermore, *Halomonas* sp. EX01 has been linked to the process of soil aggregation and enhancing the adhesion of roots to soil (RAS), thereby enhancing the ability of rice plants to absorb water and nutrients (Zhang et al., 2008).

Moreover, studies have been carried out to investigate the role of microbial strains in promoting the expansion of other crops, such as sunflower, lettuce, mustard, and pea. *Pseudomonas* sp. has been documented to enhance sunflower growth by reducing the absorption of $Na^+$ and boosting the activity of antioxidant enzymes (Tewari and Sharma, 2020). However, *Bacillus* sp. has been demonstrated to elevate mineral levels in lettuce while decreasing the concentrations of $Na^+$ and $Cl^-$ (Vivas et al., 2003). *Pseudomonas putida* RT12 has demonstrated significant enhancement in mustard growth indicators and antioxidant compounds, along with a reduction in oxidative stress markers (Alhoqail 2024). *Kocuria rhizophila* 14asp has been discovered to augment pea growth characteristics and chlorophyll concentrations, while also elevating antioxidant levels (Khan et al., 2021). These researches emphasize the numerous functions of bacterial strains in enhancing plant growth in salty circumstances across different crop species, showcasing their potential for sustainable agricultural techniques.

### *Limiting Uptake of $Na^+$ and Enhancing Beneficial Ions Uptake*

Research carried out on the types of bacteria shown in the Table 1 and Fig. 3 has demonstrated their remarkable capacity to decrease the intake of sodium while simultaneously enhancing the absorption of other essential ions. Consequently, this enhances plant development in saline settings. The microorganisms secreted extracellular polymeric substances (EPSs) that enhanced the absorption of the sodium ($Na^+$), calcium ($Ca^{2+}$), and potassium ($K^+$) ions from salts. This rise in agricultural yields, as quantified by plant dry matter, was a result of the absorption. Pseudomonas putida produces extracellular polymeric substances (EPSs) that consist of glucose, rhamnose, and mannose. It has been discovered that these substances improve tolerance to a variety of abiotic stressors, including salt stress [82]. The research conducted by Kumar et al. (2021) found that the utilization of *Bacillus pumilus* strain JPVS11 in rice farming led to a substantial reduction in the availability of $Na^+$ for plant uptake. Additionally, there was a simultaneous augmentation in the plant's growth properties, antioxidants, and photosynthetic pigments. Applying *Pseudomonas putida* RT12 to mustard plants has demonstrated the ability to reduce $Na^+$ ion absorption while promoting growth and antioxidant synthesis. This indicates that it has the ability to mitigate salt stress (Alhoqail 2024). Furthermore, the bacterium *Halomonas* sp. Exo1, which was examined in the context of rice cultivation, has demonstrated the capacity to improve plant growth attributes and elevate antioxidant levels. Simultaneously, it efficiently decreased the absorption of sodium ions, demonstrating its efficacy in lessening the antagonistic impacts of salt stress (Mukherjee et al., 2019). In addition, the research carried out by Hidri et al. (2022) revealed that *Glutamicibacter* sp. MK847981 and *Pseudomonas sp.* MK087034, when applied to Suaeda fruticose, effectively reduced the level of $Na^+$ while enhancing the absorption of $K^+$. Consequently, this resulted in an enhancement of the $K^+/Na^+$ concentration in the plants. Furthermore, the discovery of *Bacillus* sp. in crop yields as shown by plant dry weight has been found to rise with wheat farming due to enhanced uptake of sodium, calcium, and potassium ions from salts (Ashraf et al., 2004).

The research conducted by Maqsood et al. (2021) explored the impact of *Burkholderia cepacia* on the development of wheat crops. The findings demonstrated that this bacterium has the capacity to enhance chlorophyll concentrations and stimulate plant development in saline environments. These findings emphasize the potential of *Burkholderia cepacia* in saline agriculture. Furthermore, a study conducted by Han et al. (2021) revealed that the utilization of *Burkholderia pyrrocinia* on peanut plants led to a significant enhancement in both the fresh weight and root length of the plants. This emphasizes the capacity of *Burkholderia pyrrocinia* to enhance growth in saline soils. These findings highlight the significant potential of these bacterial strains to decrease the uptake of $Na^+$ while increasing the uptake of other essential ions, hence improving plant growth and productivity in saline circumstances.

### *Role of EPS-producing Bacteria in Antioxidant Production*

The research conducted on the bacterial strains indicated in the Table 1 has demonstrated their remarkable ability to enhance antioxidant levels in plants. Consequently, this enhances the plants' capacity to endure oxidative stress triggered by salt. The research conducted by Haque et al. (2022) demonstrated notable improvements in antioxidants, as well as enhancements in morphological parameters and relative water content, in tomato cultivation through the application of *Bacillus subtilis* ESM14 and *Pseudomonas putida* ESM17. The study on wheat cultivation demonstrated that the presence of *Bacillus methylotrophicus* PM19 had a positive effect on the levels of antioxidants. In addition, it enhanced the process of seedling germination, as well as the length of both the roots and shoots. Furthermore, it also had a positive impact on the production of photosynthetic pigments (Amna et al., 2019). A study conducted by Sun et al. (2020) revealed that the utilization of *Pantoea alhagi* NX-11 in rice cultivation resulted in a notable enhancement in antioxidant activity. As a result, plant growth was improved in saline conditions. The study conducted by Mukherjee et al. (2019) found that *Halomonas* sp. EX01, a bacterium studied in the context of rice agriculture, has the capability to improve plant development traits and boost antioxidants, thereby mitigating the effects of salinity stress. A study on sunflower cultivation demonstrated the efficacy of *Pseudomonas putida* in decreasing the uptake of $Na^+$ and enhancing the functionality of antioxidant enzymes. According to Tewari and Sharma (2020), *Pseudomonas putida* has the ability to decrease oxidative stress. Furthermore, the study conducted on mustard plants revealed that *Pseudomonas putida* RT12 displayed enhanced levels of antioxidants and demonstrated improvements in growth indices. This underscores its efficacy in mitigating oxidative stress induced by salt (Alhoqail 2024). *Kocuria rhizophila* 14asp, which was investigated in the context of pea farming, demonstrated improved growth traits and elevated levels of chlorophyll. Additionally, there was a notable increase in antioxidants, suggesting their potential to enhance plant resilience against oxidative stress (Khan et al., 2021). The results emphasize the significant capacity of these bacterial strains to enhance antioxidant levels in plants, thereby reinforcing their resistance to oxidative stress induced by salinity.

### *EPS Role in Soil Aggregation*

Furthermore, it has been observed that these EPSs have a role in the process of soil aggregation, as shown in Table 2 [83]. Vaishnav et al. (2016) undertook a study to examine how the PGPR *Pseudomonas simiae* strain AU, which is recognized for its ability to create biofilms, affects the transcription of salt-resistant genes in soybean plants when they are exposed to salinity stress. In comparison to the control group that did not have salt, the researchers found that the presence of salt increased the expression of all genes except for nitrate reductase (Fig. 4). *P. simiae* treated salty soil seedlings showed a considerable increase in the relative expression of defense proteins (vegetative storage protein) and antioxidant enzymes (peroxidase and catalase), especially when sodium nitroprusside, a nitric oxide donor, was present. Bacterial presence in both non-saline and saline soils led to the suppression of the high-affinity potassium transporter. The relative expression of lipoxygenase and polyphenol oxidase increased in saline soil treated with bacteria, although the rise was

Table 2. EPS-producing bacterial strains involved in aggregation of rhizo spheric soil.

| Bacterial strain | Role in amelioration of salinity | References |
|---|---|---|
| *Bacillus amyloliquefaciens p16* | Not only does it confer acid tolerance to the bacteria, but it also enhances soil aggregation when applied to the soil. | [114] |
| *Bacillus insolitus* MAS10 | Enhanced soil aggregation was seen in the vicinity of the roots of the wheat plants that were infected. | [34] |
| *Bacillus proteolyticus A27* | *Strains enhanced the proportion of water-stable macro-aggregates.* | [115] |
| *Bacillus tequilensis* and *Bacillus aryabhattai* | The primary types of carbohydrates contributing to soil aggregation were identified as EPS and glucose. | [97] |
| *Halomonas eurihalina ATHM 37* | Not only does it confer acid tolerance to the bacteria, but it also helps to enhance soil aggregation when added to the soil. | [116] |
| Halomonas variabilis (HT1) and Planococcus rifietoensis (RT4) | Improved the soil aggregation in the roots of plants that were inoculated. | [117] |
| *Methylobacterium oryzae CBMB20* | Minerals are concentrated near the root, and their absorption is improved. | [118] |
| *Paenibacillus mucilaginosus VKPM B-7519* | These bacteria are capable of silicate weathering, a process in which they release a large amount of nutritional ions from minerals and soil. | [39] |
| *Pseudomonas putida X4* | Improved soil aggregation and presence of minerals such as kaolinite, montmorillonite, and goethite. | [119] |
| *Rhizobium phaseoli* Mn-6 | An efficient approach to enhance plant growth, physiology, yield, and soil physical properties. | [59] |

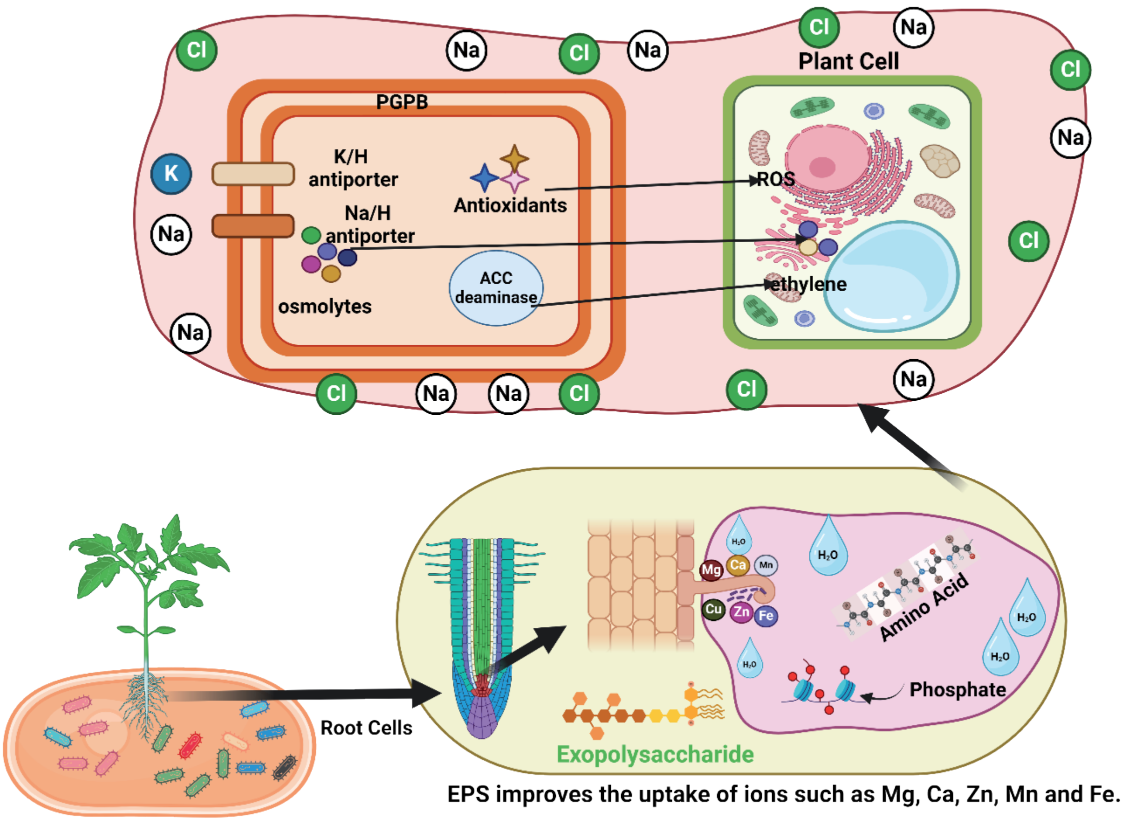


Fig. 3. Salinity stress leads to the uptake of maximum Na ions, which are limited by EPS-producing bacterial strains. Also, the useful ions are increased by PGPB, which leads to enhanced plant growth.

less significant compared to the non-inoculated saline reference. This observation suggests that there might be distinct mechanisms involved in controlling the expression of genes related to defense and antioxidants when exposed to high levels of salt. When soybean plants are exposed to salinity stress, researchers have seen a notable increase in their growth, especially when *P. simiae* and the nitric oxide donor are present. In their study [84], it was shown that soybeans and common beans exhibited comparable outcomes when they were simultaneously inoculated with rhizobia and azospirilla. The soil endosphere, rhizoplane, and rhizosphere each contain unique collections of microorganisms. A mutually beneficial growth for microorganisms and plants is facilitated by the creation of root-microbe interaction. The presence of abiotic variables, such as salinity stress, in the soil leads to the development of biofilms and the creation of extracellular polymeric substances (EPSs) by soil microflora. These processes contribute to the aggregation of soil particles. This process improves the absorption of nutrients in plants and helps the concentration of salt ions in the polysaccharide network. As a result, it reduces the negative impacts of salt stress on plants [85]. It has been demonstrated that applying strains of *Oceanobacillus kapialis* PGPR and *Thalassobacillus denorans* to crop plants grown in salty environments enhances biomass output, plant vitality, nutrient absorption, and seed germination.

Thus, growing bacteria that promote plant growth and plants together in salty soils can both mitigate the consequences of saline stress and increase crop productivity. This approach provides an economically efficient and ecologically sound method for addressing salt stress [36]. The examination of bacterial strains presented in the Table 2 has provided insight into their essential role in promoting soil aggregation, hence enhancing soil structure and fertility in saline environments. In the study conducted by Qurashi and Sabri (2012), it was discovered that the use of *Halomonas variabilis* (HT1) and *Planococcus rifietoensis* (RT4) in chickpea cultivation resulted in a notable improvement in soil aggregation. Consequently, this led to an enhancement in the absorption of nutrients by plants, which ultimately resulted in improved plant development, especially in high salt stress circumstances. The investigation on *Halomonas* sp. EX01, conducted in the context of rice agriculture, revealed its involvement in soil aggregation and the enhancement of root adherence to soil (RAS). This facilitates the efficient absorption of water and nutrients by plants, particularly in areas with high salt content (Zhang et al., 2008). These data highlight the significant influence of these bacterial strains on improving soil structure and boosting nutrient availability, demonstrating their potential for promoting sustainable agriculture in saline conditions.

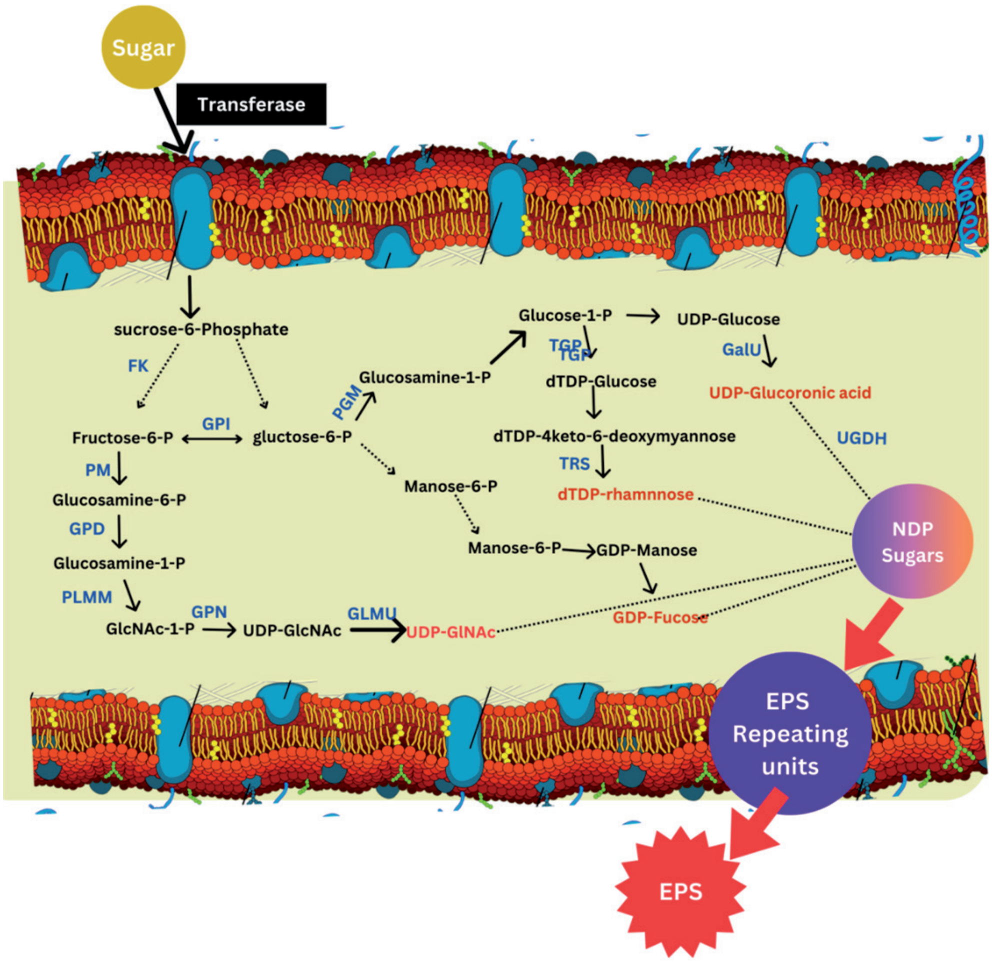


Fig. 4. Shows the mechanism by which *S. thermophilus*, a particular strain of bacteria, utilizes sugar to produce EPS (extracellular polymeric substances) through a unique metabolic pathway. The information is derived from research conducted by Cui et al. (2016). What does the abbreviation FK stand for fructokinase, GalE is UDP-galactose-4-epimerase, GalK is galactokinase, GalT is galactose-1-phosphate uridylyltransferase, GalU is UDP-glucose pyrophosphorylase, and GK is glucokinase. GLMU is an abbreviation for N-acetylglucosamine-1-phosphate uridyltransferase. GPD stands for glucosamine-6-phosphate deaminase. GPI represents glucose-6-phosphate isomerase. GPN refers to glucosamine-1-phosphate N-acetyltransferase. LacZ is an enzyme called β-galactosidase. MPI is an enzyme called mannose-6 phosphate isomerase. PEP is an abbreviation for phosphoenolpyruvate. PGM: Alpha-phosphoglucomutasePLMM refers to phosphoglucosamine mutase, while PM stands for phosphomutase. The following enzymes are involved in several biochemical processes: FmlB, which is responsible for converting dTDP-glucose to 4,6-dehydratase; SPH, which hydrolyzes sucrose-6-phosphate; TGP, which catalyzes the pyrophosphorylation of dTDP-glucose; TRS, which epimerizes dTDP-4-dehydrorhamnose; UDP-GalNAc, which is UDP-N-acetylgalactosamine; UDP-GlcNAc, which is UDP-N-acetylglucosamine; UGDH, which is UDP-glucose 6-dehydrogenase; and UGM, which is UDP-galactopyranose mutase.

### *The Role of Bacterial Strains in Enhancing Photosynthetic Efficiency*

Bacterial strains, specifically *Bacillus tequilensis* and *Bacillus aryabhattai*, have been recognized for their capacity to improve photosynthesis in rice plants. These strains enhance photosynthetic rates by enhancing nutrient availability and water uptake in the rhizosphere, resulting in a greater yield (Shultana et al., 2020). *Kocuria rhizophila* 14asp is a bacterium strain renowned for its capacity to enhance the chlorophyll levels in pea plants. This strain enhances the plant's photosynthetic efficiency and overall development by altering the rhizosphere environment, leading to increased chlorophyll production (Khan et al., 2021).

### *Increasing Relative Water Content and lowering MDA and $H_2O_2$*

The bacteria Bacillus subtilis susp. *Inaquosorum* and *Marinobacter lipolyticus* SM19 have demonstrated the ability to enhance the relative water content (RWC) in wheat plants. These strains enhance water retention in plant tissues, leading to increased hydration and overall plant health (Talebi Atouei et al., 2019). *Pseudomonas putida* RT12 has been recognized for its capacity to decrease the levels of malondialdehyde (MDA) and hydrogen peroxide ($H_2O_2$) in mustard plants. The bacterial strain mentioned in the study (Alhoqail 2024) improves plant development and antioxidant defenses by reducing oxidative stress.

*Role in Protecting Root from High Salinity*

Bacteria that flourish in environments with high salt concentrations generally release extracellular polymeric substances (EPS) surrounding their cells. EPSs have the ability to stick to the soil and encourage the growth of big pores in the soil, increasing the fertility of land used for farming. Therefore, these strains can be classified as PGPR strains because of their advantageous influence on the development of plant growth and agricultural productivity. [86]. The combination of soil and extracellular polymeric substances (EPS) created by microorganisms has the capacity to improve fertility in the rhizospheric zone, hence enhancing the accessibility of nutrients to crops [87]. Bacterial extracellular polymeric substances (EPS) have a favorable capacity for water retention. Therefore, plants that are treated with EPS demonstrate significant resistance to abiotic stresses, such as drought and salinity [80]. The existence of bacteria that produce exopolysaccharides (EPS) in the area around the roots of plants leads to a decrease in the presence of sodium ions ($Na^+$) in the region of soil immediately surrounding the roots. As a result, this reduces the level of stress caused by high salt concentrations [88]. Therefore, it is well accepted that EPS reduces the amount of NaCl in the soil and promotes the optimal growth of plants used in agriculture. Hence, employing bacteria that generate EPS to mitigate salt stress could serve as a novel and cutting-edge approach to rejuvenate degraded soil.

## Conclusions

EPS-producing bacteria are essential for reducing the negative effects of salt-induced stress on plants, making them a critical element of sustainable farming methods. This is particularly important due to the substantial impact of salinity stress on crop productivity. This review identified several critical aspects: These bacteria enhance plant growth in various crops, including wheat, maize, tomato, rice, sunflower, lettuce, mustard, pea, and faba bean. By enhancing antioxidant levels, boosting the uptake of advantageous ions, and reducing salt absorption, they achieve this. In addition, bacteria that produce EPS (Exopollysacharides) play a vital role in decreasing salt intake and enhancing the absorption of essential ions. Consequently, this facilitates the proliferation of plants in environments that have elevated salt levels. Furthermore, these bacteria play a crucial role in the process of soil aggregation, enhancing the structure and fertility of soil in saline conditions. As a result, they enhance the absorption of nutrients and reduce the negative impacts of salt stress. Furthermore, numerous bacterial strains have exhibited the capacity to enhance the efficacy of photosynthesis in plants, leading to increased productivity and agricultural yield. Furthermore, the presence of bacteria that generate EPS not only increases the water content of plants but also mitigates oxidative stress and protects roots from excessive salt, hence promoting plant health and improving their ability to withstand stress.

Subsequent investigations may enhance the application of these bacteria in farming, investigate their relationships with various crops and soil compositions, and create environmentally acceptable biocontrol methods to lessen the consequences of salt stress and restore damaged soils. In addition to promoting environmental sustainability, this would improve food security worldwide.

In conclusion, EPS-producing bacteria offer a promising, sustainable solution to mitigate the harmful effects of salinity on crops. Further research should focus on optimizing their application across diverse crops and soils to enhance food security and promote environmentally friendly farming practices.

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## Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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