A REVIEW: HARNESSING SALT-TOLERANT PLANT GROWTH-PROMOTING RHIZOBACTERIA FOR SUSTAINABLE AGRICULTURE

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-----ABSTRCT------

The salinity of the soil is becoming a major concern for the world's food security. it is essential to create environmentally friendly sustainable techniques that boost saline soil productivity. Certain microorganisms have a dependency on salt as well as tolerance to it. Microbes that are resistant to salt may withstand ionic and osmotic stress. From very alkaline, saline, and sodic soils, many genera of salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) have been discovered. Numerous them are also known to help plants cope with a range of biotic and abiotic stressors. The possibility of using ST-PGPR to improve the productivity of plants under salt stress has been studied in the past several years, indicating that saline agro-ecosystems can be restored through its use. This review will focus on ST-PGPR and how they might boost saline agro-ecosystem production. Additionally, it sheds light on future research directions on the use of ST-PGPR for saline soil reclamation and PGPR-mediated mechanisms of salt tolerance in various crop plants.

KEYWORDS: saline soils, salt tolerant, PGPR mechanism, sustainable development, sodic soil------

1. INTRODUCTION

6.73 Mha land of India is damaged by salt. Of this, 16 states receive 2.95 million hectares of salinity. A major threat to the sustainability of the crop production system is the potential more than twofold increase in salt-affected soils (SAS), which are currently distributed over 6.73 million hectares (Mha) in India by 2050, according to research conducted by the Central Soil Salinity Research Institute (CSSRI). Currently, there is scientific consensus that the human production model and energy consumption have an effect in climate change [1]. Recent research shown that 20% of raised land and 33% of irrigated land are vulnerable to high salinity, with a predicted rise of 10% each year. More than 1.257 million hectares of soil are affected by salt [2].

Global climate change generates adverse environmental conditions, including salinity in soils, severe temperatures, droughts, and floods, limiting plant species spread and crop production [3, 4]. Severe weather conditions negatively impact the environment, economy, and society, particularly in semi-arid regions, while arid land degradation is a consequence of the Green Revolution's excessive use of synthetic substances [5,6]. The global agricultural system's primary objective is to increase output, but negative environmental effects must be reduced through rethinking existing and future approaches and developing sustainable technology [7]. Among the methods developed by scientists are the breeding of salt-tolerant crops, the physical removal of salts from the soil's surface, and the chemical treatment of the soil [8,9]. By controlling hydric resources and their quality, sustainable land management, although gradual and expensive, can lessen the consequences of soil salinity [10,11].

Plant growth-promoting rhizobacteria (PGPRs) are a vital component of organic agriculture. Their presence in the rhizosphere is crucial for improving soil production, promoting plant development, and squelching plant diseases. The majority of promising and extensively documented genera of photosynthesis-generating bacteria (PGPR) comprise *Pseudomonas, Aeromonas, Klebsiella, Azoarcus, Enterobacter, Azospirillum, Clostridium, Azotobacter, Arthobacter, Rhizobium, Gluconacetobacter, Bacillus,* and *Serratia* [7].

2. PROBLEM OF SOIL SALINIZATION

While it is known that soil salinity is a concern on every continent in the world, a reliable map of the locations and distribution of salty soils is lacking. The majority of crops in these regions are irrigated, and to make matters worse, poor irrigation management causes secondary salinization, which threatens 20% of irrigated land globally [12]. Poor-quality groundwater is being utilized for irrigation to produce more on each hectare of arable land that



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is available [13]. Almost 70% of ground water is used for agricultural globally, but when it is depleted, lowerquality water is used instead [14]. Salt-affected soil solenchak and solonetz are identified by the soil map legend and are distinguished by an accumulation of highly soluble salt. Its EC varies from 8 to 15 dS/m1 and it is found in semi-arid coastal regions.[15]. Unsustainable groundwater withdrawals decrease crop quality and range, often rendering a region unusable for cultivation, and cause waterlogging, soil toxicity, and acidity [16]. salinity diminishes agricultural productivity of cereals, legumes, forages, and horticultural crops, while also affecting soil microbial ecology and physicochemical qualities. Salt stress can lead to reduced agricultural productivity, increased soil erosion, and lower economic returns [17]. Plants have physiological changes due to salinity stress, including stomatal closure, early senescence, reduced photosynthesis, and increased oxidative damage [18]. For actual use, salt-affected areas are classified as saline, alkali, sodic, saline-alkali, or saline sodic. Saline soil has an excess of soluble salt in the soil solution, which is the liquid that exists between soil particles [19]. Solonetz soils—also referred to as alkaline or sodic soils—have a pH above 8.5 and are very alkaline. They are found on 135 million hectares around the world in semi-arid temperate continental climates, including China, Argentina, Kazakhstan, Hungary, Bulgaria, Romania, and the Ukraine [15]. Plant development is hindered by salinity, which is caused by the buildup of dissolved salts in soil water, either naturally or by human activity [20].

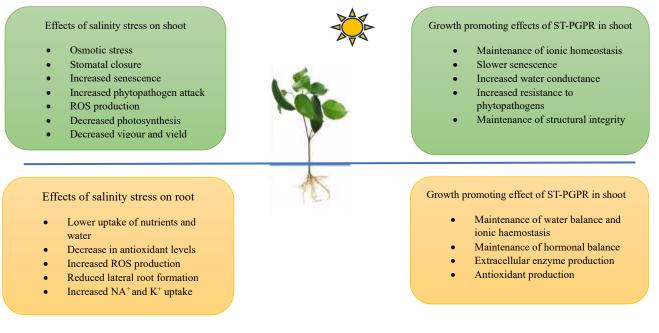


Figure 1. Effects of salinity stress and associated tolerance mechanisms induced by salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) in both plant roots and shoots.

According to estimates, saline soil covers around 7 million hectares of land in India, which includes Punjab, Haryana, Uttar Pradesh, Bihar, and portions of Rajasthan [21]. Soil salinity not only hinders plant growth and development, but it also has a negative influence on microbial composition, variety, and functions [22].

3. IMPACT OF SALINITY ON PLANTS

Soil salinity poses a risk to plant health. Salinity alters the blooming and fruiting patterns, causing a disruption in reproductive physiology that, in turn, impacts crop yield and biomass [23]. Plant development is inhibited by salinity stress, which affects physiological and metabolic processes including water stress, ion toxicity, nutritional problems, oxidative stress, altered metabolic processes, membrane disruption, reduced cell division and expansion, and genotoxicity based on severity and duration. [24]. Salt-affected soil consists of saline soil, sodic soil, and saline-sodic soil [25]. Plant phosphorus (P) absorption is considerably reduced by soil salinity, since phosphate ions precipitate with Ca ions [26]. High salt stress (150 mm NaCl) in tomato has been demonstrated to affect flowering transition time, producing a delay in the first inflorescence as well as a reduction in shoot and root formation [27]. Deferred blooming in chickpea is directly associated with increased Na⁺ concentrations in the laminae of fully expanded leaves [28]. Interestingly, the Salt Overly Sensitive (SOS) route is an important protective system linked with Na⁺ ejection and maintaining particle homeostasis at the cell level [29,30]. However, salt stress has been demonstrated in multiple studies to deactivate SOS, photoperiodical, and circadian clock switch proteins associated with flowering [31,32,33]. The primary cations linked with salinity are Na⁺, Ca²⁺, and Mg²⁺, while the most prevalent anions are Cl, SO4⁻², and HCO3 [34]. Salinity stress increases signal perception



and transduction, restricting Na+ uptake and accumulation, while osmotic stress tolerance is mediated by a decrease in stomatal conductance.[35]. Accumulation of Na⁺ ions in plant tissues causes the generation of reactive oxygen species (ROS), including singlet oxygen ($_{1}O^{2}$), hydrogen peroxide (H₂O₂), superoxide (O.⁻²), and hydroxyl radical (OH), which impede photosynthesis [36]. Compared to other ions like Ca2+, Mg2+, or K+, sodium is a highly poisonous and soluble ion that is extensively disseminated and ineffectual in causing salinization in plants. [37]. Certain elements, especially sodium, chlorine, and boron, can be hazardous to plants. Excessive sodium buildup in cell walls can swiftly promote osmotic stress and cell death [38]. Plants grow well in salty conditions, but osmotic equilibrium is essential for development because it keeps cells from drying up and dying.[39]. A high concentration of K⁺ is also necessary for tRNA binding to ribosomes and consequently protein synthesis. and cannot be replaced by Na⁺. However, ion toxicity caused by the substitution of K⁺ by Na⁺ in metabolic processes make it unavailable for the process. [40,41]. The detrimental effects of salinity are due to stress on differentiation and the cell cycle, which results in fewer cells and limits growth. Additionally, it has a deleterious effect on all aspects of plant development, including mitosis, DNA, RNA, enzyme activity, and seed germination [42,43,44].

4. MECHANISMS OF SALINITY TOLERANCE/RESISTANCE INDUCED BY PGPB

Crop production is significantly reduced by salinity's physiological impacts [1,45]. On the other hand, it has been demonstrated that applying Plant Growth Promoting Bacteria increases crop production by lessening the physiological harm brought on by high soil ion concentrations [1,46]. Elevated ion concentrations inside the cytoplasm cause an ionic imbalance, which in turn preserves the K⁺ osmotic equilibrium, triggers osmotic reactions, and activates genes involved in adaptive, metabolic, protective, and amino acid transport pathways. Furthermore, the synthesis of organic solutes (alanine, serine, glutamic acid, sucrose, choline, and betaine) [47,48] bolster the osmotic force inside cells to stabilize macromolecules within cells during salt stress [49]. In general, direct and indirect mechanisms make up the two subtypes of PGPB modes of action. In direct mechanism, organisms reside inside plants to have an impact on plant metabolism, indirect organisms are thought to be external [50] By functioning as hormone sinks and releasing growth factors, microbes enhance adaptability through indirect mechanics. By regulating secondary metabolites and signal susceptibility, indirect mechanisms help increase resistance to pathogen invasions and stress [51,52]. The role of halotolerant plant growth-promoting rhizobacteria (HT-PGPR) in reducing salt stress in agricultural plants has grown in the last several years.

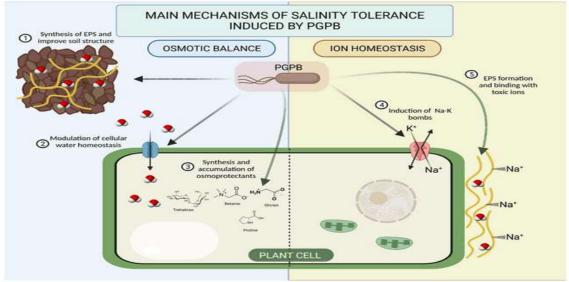


Figure 2. Main mechanisms of salinity stress tolerance induced by Plant Growth Promoting Bacteria (110).

By directly producing a variety of advantageous metabolites, including exopolysaccharides, siderophores, volatile organic compounds (VOCs), compatible osmolytes, and phytohormones, or indirectly by controlling the expression of stress-related genes and thwarting the effects of phytopathogens, ST-PGPR increase the productivity of the saline-agroecosystem (Figure 3) [53,54].

4. DIRECT MECHANISMS

Indole-3-Acetic Acid production

Plant growth regulators, sometimes referred to as phytostimulators, are substances that naturally possess the capacity to control the synthesis of certain growth regulator enzymes and have a significant impact on many aspects of plant growth, including the morphological, physiological, and biochemical processes of the plant [55]. Indole acetic acid, which is necessary for cell division and elongation in plants under salt stress, is produced by

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the ST-PGPR. *Azotobacter, Arthrobacter, Azospirillum, Pseudomonas, Stenotrophomonas*, and *Rahnella* are a few of those most renowned ST-PGPR generating IAA under salt stress [56,57,58]. Assessing the mode of action of various phytopathogens has shown that while excessive concentrations of IAA can be hazardous, at appropriate levels they may have positive benefits [1,59]. With its help, we may be able to identify the PGPR strain utilizing bacteria that release IAA [60]. One of the most significant plant hormones, IAA controls a wide range of processes related to plant growth and development across the course of the cell cycle, including root initiation, apical dominance, blooming, fruit ripening, and senescence, as well as cell division, elongation, and differentiation. [61] Further, by boosting the availability of water and nutrients to plants, salt-tolerant Rhizobacteria increases the production of IAA in plants, reducing the growth of tap roots, encouraging the elongation of root hairs, and lengthening lateral roots.[62]. The role of IAA in resistance to increased salt stress was demonstrated by Numan et al. (2018), who observed abundant IAA generation with osmotolerant PGPR *Azospirillum brasilense* NH at high salt concentration in durum wheat. It is well known that maize growth is enhanced by desiccation-tolerant Microocccus luteus when IAA is produced [63,64]. Since the synthesis of phytohormones is a critical trait of PGPR that may be exploited, more research must be done to determine how to employ PGPR to mitigate the negative impacts of salinity [65].

Symbiotic Nitrogen fixation

For plants to develop and be productive, nitrogen (N) is the most important nutrient but developing plants cannot use it. By employing a sophisticated enzyme system called nitrogenase involving a process known as biological N_2 fixation (BNF), which transforms atmospheric N_2 into forms that plants can use [66]. Symbiotic bacteria found in legume nodules are believed to be the most crucial element in the biological fixation of atmospheric nitrogen.[67]. Numerous bacterial species have been shown to be connected to the plant's rhizosphere, which further promotes the growth of the plant. It encompasses the following, *Erwinia, Azospirillum, Flavobacterium, Bacillus, Arthrobacter, Rhizobium, Acinetobacter, Burkholderia, Pseudomonas, Enterobacter, and Serratia* [68,69]. Around the world, biological nitrogen fixation generates 180 X 106 metric tons annually, of which symbiotic relationships generate 80% and free-living or associative systems the remaining portion.[70]. In two years, a rice rhizosphere strain of A. radiobacter greatly boosted yields of barley and winter wheat (5–30%) and contributed 23–32% to total nitrogen absorption. [111].

Non-symbiotic nitrogen-fixation

It has been shown that when soil contains mineral nitrogen, free-living nitrogen-fixing bacteria consume the nitrogen instead of fixing it [71,72]. It is essential to both agriculture and the fixing of nitrogen. An energy-oriented fixation of nitrogen in a form that plants might easily use has been the main obstacle obscuring its effect. By putting them closer to the roots, the constraint might be readily overcome. Numerous bacteria are linked to non-symbiotic nitrogen fixation, including but not limited to *Azoarcus* sp., *Herbaspirillium* sp., and *Azotobacter* sp., [73,74]. Soil bacteria can convert mineral nitrogen into gases like NO, N2O, and N2, which harms agroecosystems. Nitrogen metabolism genes in soil bacteria are influenced by nitrogen availability, potentially aiding nitrogen accumulation.[75]. Noori et al.'s 2019 study also examined the impact of effective isolates on plant development under salt stress. The isolates included rhizobial and non-rhizobial bacteria that are tolerant of salinity and drought from surface-sterilized alfalfa root nodules cultivated in salty soils. They simultaneously injected K. cowanii A37, S. meliloti ARh29, and *Klebsiella sp.* A36 into the alfalfa plant. According to the findings, nitrogen could be supplied to plants by *Klebsiella sp.* A36 and *Kcowanii* A37 and increased plant growth indices in the absence of rhizobial bacteria [112].

Phosphate solubilization

Phosphorus is the second most essential element in plant nutrition, behind nitrogen. The pH, compaction, aeration, moisture, temperature, texture, and organic matter of soils, crop residues, the size of plant root systems, root exudate secretions, and soil bacteria that are present all affect how much phosphorus is accessible to plants [76]. As rescue mechanisms, soil microbes contribute to soil acidification and consequent solubilization of inorganic phosphates. Among the most common are phosphorus-solubilizing bacteria from the genera *Bradyrhizobium*, *Cladosporium, Azotobacter, Bacillus, Pseudomonas, and Enterobacter* [77]. Phosphoric fertilizers are widely used in agricultural areas to compensate for the soil's *Pseudomonas* deficiency. Plants absorb less phosphatic fertilizer, and what is left over is rapidly converted by the soil into insoluble complexes [78]. Not only bacteria but fungi from the following groups are also taken into account: *Achrothcium, Alternaria, Arthrobotrys, Aspergillus, Cephalosporium, Chaetomium, Cladosporium, Cunninghamella, Curvularia, Fusarium, Glomus, Rhizopus, Saccharomyces, Schizosaccharomyces, S chwanniomyces, Sclerotium, Torula, Trichoderma, and Yarrowia. Of all the microorganisms that can solubilize phosphate, bacteria make up as much as 50% of the total, whilst fungi make up as little as 0.5% [79].*



Exo-polysaccharides (EPS) production

One common trait shared by several rhizosphere bacteria is the production of surface polysaccharides, or EPS. Even though the quantity and makeup of EPS might fluctuate throughout ST-PGPR strains, unfavourable circumstances lead to the formation of large amounts of EPS [80,81,82]. The synthesis of exopolysaccharides (EPS) also gives bacteria a means of preventing plants from absorbing harmful ions by enclosing the root system in a physical barrier, these chemicals mitigate the consequences of the ion toxicity phase [11,83,84]. The generation of EPS promotes the growth of biofilm, which in turn promotes soil aggregation and moisture retention [85] Stress affects EPS production. In E. coli, LonS, an ATP-dependent enzyme that denatures proteins under stress, regulates ResA, a positive transcriptional regulator. [86]. Additionally, the production of exopolysaccharides may improve the odds of bacterial survival in desiccation or nutrient-deprived environments, as well as aid in nitrogen fixation by limiting excessive oxygen tension. These polysaccharides may also be implicated in cell aggregation [87].

Siderophore production

Approximately 140 enzymes require iron as a cofactor, necessary for cytochrome and ribonucleotide reductase. It occurs in the forms of oxyhydroxides, insoluble hydroxides, and ferric Fe³⁺ under circumstances of plentiful O₂, none of which are accessible to microorganisms or plants [88]. Low molecular weight molecules called siderophores bind iron (Fe+++) and move it across the cell membrane. The iron siderophore complex enters cells by bacterial absorption, facilitating the growth of microorganisms. The majority of the Fe+3 in the rhizosphere is bound by siderophores produced by soil bacteria, avoiding fungal diseases.[89]. The capacity of rhizobacteria to use siderophores generated by various genera of rhizobacteria is often variable; some are skilled at using siderophores produced by the same species (homologous siderophores), while others may be able to use those produced by other rhizobacteria (heterologous siderophores) [90]. Winkelman and Dreschel (1997) recognised five kinds of siderophores, formerly known as sideramines and sideromycins, which are iron chelators classified into hydroxamates and techolates.[91]. Therefore, excessive soil concentrations of heavy metals cause stressors on plants, which are lessened by bacterial siderophores [88]. In 2007, Crowley and Kraemer discovered that oat plants had a siderophore-mediated iron transport system. They deduced that siderophores generated by rhizosphere is no to oat, which possesses mechanisms for using Fe-siderophore complexes in situations where iron availability is restricted [114].

HCN production

It is during the early stationary growth phase that hydrogen cyanide is generated [92]. The volatile chemical hydrogen cyanide (HCN) is released by *Pseudomonas*. Along with their protective function for the host plant, they have antibacterial actions [94]. In solution, cyanide takes the form of free cyanide, which consists of the nondissociated HCN and the cyanide anion (CN⁻). Cyanide, a phytotoxic chemical that may disrupt key metabolic enzymes, is thought to be a common characteristic of harmful rhizobacterial isolates [95]. A broad-spectrum antibacterial substance called HCN is used in the biological management of root infections [96]. Glycine is used to create this element together with CO_2 [97]. According to Qurashi and Sabri (2012a), chickpea growth, soil structure stability, and aggregation under salt were all enhanced by EPS-producing ST-PGPR *Halomonas variabilis* (HT1) and *P. rifietoensis* (RT4) [93].

Ammonia production

The generation of ammonia is mostly seen in leguminous rhizobacteria and is associated with nitrogen fixing. A variety of rhizobacteria that promote plant development interact with C3 and C4 plants (such as cotton, rice, wheat, maize, sugarcane, Jatropha, and so on) to greatly enhance their vegetative growth and grain output [98]. A variety of aerobic heterotrophic bacteria called Azospirillum species proliferate widely in the rhizosphere of gramineous plants, fixing nitrogen in microaerobic circumstances. ¹⁵N tracer methods revealed that through biological nitrogen fixation, *Azospirillum lipoferum and Azospirillum brasilense* provided 7–12% of the N in wheat plants [98,99]. In greenhouse studies (Muthukumarasamy et al. 1999) are inoculation with Azospirillum also significantly enhanced the N content of sugarcane leaves, a reflection of Azospirillum's ammonia production [113].

8. INDIRECT MECHANISMS

Rhizobacteria's primary indirect method of promoting plant development is via serving as biocontrol agents [100]. In general, the main biocontrol mechanisms in PGPR are nutritional competition, niche exclusion, induced systemic resistance, and the synthesis of antifungal metabolites [101]. It has been documented that a wide variety of rhizobacteria create antifungal metabolites, including phenazines, pyrrolnitrin, 2,4-diacetylphloroglucinol, pyoluteorin, viscosinamide, and tensin [102]. On the other hand, secondary metabolites and their sensitivity to signals generated by the microbe are relayed by an indirect process. It involves, for instance, the development of tolerance to various stress circumstances as well as resistance to a variety of pathogen attacks [103]. Additionally,



ethylene and jasmonate signaling occur inside the plant during ISR, and these hormones activate the host plant's defensive mechanisms against a range of plant diseases [105]. In order to improve soil richness, this method uses a variety of tools, such as the production of hydrolytic proteins, anti-microbials, and more, to reduce the need for agrochemicals (pesticides and manures). It also addresses a wide range of misuses of plant development that elevate rhizobacteria [104].

9. FUTURE PROSPECTS

Salt tolerance is increased by symbiotic bacteria in the rhizosphere and roots of plants; however, it is uncertain if halophyte rhizobia can be successfully introduced to non-halophyte plants over the long term.[106]. On the one hand, a more varied group of microorganisms might offer more advantages to plants [107]. However, certain PGPB strains may concurrently display a number of actions that promote plant development. For instance, it has been reported in a number of articles that bacteria that fix nitrogen are capable of phosphate solubilization among other things. On the other hand, it is unknown how actively a single bacterial strain may display many characteristics that are advantageous for plant development at the same time [108]. The research looks at metabolites and genes related to salt tolerance, investigates salt-stressed plant growth strategies utilizing -OMICs techniques, and investigates the effect of PGPR on plant epigenome alteration.[109]. In resent year, an growing amount of research studies has confirmed the clear relevance and importance of bacterial consortia by focusing on their application and having a beneficial impact on plant growth and development.

10. CONCLUSION

The increasing population and demand for food have led to increased agricultural production, but saline stress is a major obstacle. PGPRs provide a reliable solution by accelerating plant development, seed germination, and protection against environmental stressors. Salt-tolerant rhizobacteria can reduce salt stress while plants grow. Further research is needed to confirm the effectiveness of PGPR formulations on different plant species and genotypes. PGPRs can improve agricultural productivity by enhancing soil fertility and plant nutrition through nutrient acquisition.

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