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Review

The Role of Plant Growth–Promoting Halobacteria in Mitigating Abiotic Stress and Improving Crop Performance in Saline Soils

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Abstract

Arid and semi-arid soils often have low agricultural productivity because of abiotic stresses such as drought and salinity. Halobacteria have been shown to enhance crop yields under these stressful conditions. These microorganisms can survive across a broad range of salinity levels (1–25% NaCl), including environments without NaCl, and they promote plant growth through both direct and indirect mechanisms. This review compiles research from the last five years examining the influence of halobacteria on plant performance and soil fertility. It also evaluates the criteria used to select halobacteria for such studies. Only a limited number of investigations have focused on their effects on soil fertility. Most selection approaches rely on qualitative traits, such as colony morphology on salt-enriched media, primarily containing Na^+. However, not all bacteria that grow in saline media are capable of binding or sequestering Na^+ ions. Consequently, a quantitative selection criterion—such as the in vitro ability to capture Na^+ ions—should be adopted. Incorporating this criterion, along with systematic evaluation of halobacteria's impact on soil fertility, could significantly aid in the restoration of saline soils.

Keywords: abiotic stress; drought; plant growth-promoting rhizobacteria; salinity; soil fertility

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Introduction

Abiotic stresses such as salinity, drought, extreme temperatures, and heavy metal contamination significantly reduce agricultural productivity [1]. Climate change has intensified both the occurrence and severity of these stress factors, with rising temperatures and reduced rainfall contributing to increasingly severe drought conditions [2]. Current estimates suggest that abiotic stress is responsible for up to 50% of global crop yield losses [3]. According to Etesami and Maheshwari [2], soil salinity alone causes an annual reduction of 1–2% in arable land. Arid and semi-arid regions are particularly vulnerable, as drought and salinity frequently occur together and are closely interconnected. Soil salinization refers to the accumulation of soluble ions, including Na^+, Ca^{2+}, Mg^{2+}, and K^+, resulting from limited rainfall and high temperatures. Agricultural practices further exacerbate soil salinity through the use of low-quality irrigation water, inefficient farming methods, and excessive application of chemical fertilizers and pesticides [4,5], ultimately degrading soil fertility and quality.

Drought stress negatively impacts crop yields by restricting water availability, which in turn disrupts photosynthesis, nutrient absorption, and plant metabolic processes [6]. To address these challenges, numerous studies have explored various strategies, such as improving conventional agricultural practices, developing new crop varieties, applying genetic engineering techniques, and utilizing biostimulants to mitigate yield losses caused by abiotic stress [1]. However, breeding and genetically engineering crops for resistance to salinity and drought remain complex and time-consuming processes, as these stresses affect multiple physiological pathways within plants and require long-term research efforts [7]. In contrast, biostimulants have demonstrated beneficial effects in enhancing plant tolerance to abiotic stress conditions [8]. The excessive use of fertilizers and pesticides has markedly diminished soil microbial diversity and contributed to environmental pollution. Moreover, certain synthetic agricultural inputs have been restricted due to their uptake and accumulation of toxic compounds in plant tissues, which pose potential risks to human health [9]. A sustainable and environmentally sound approach to agriculture involves the application of inoculants containing beneficial microorganisms that promote plant growth or protect crops from pathogens and abiotic stresses [9]. Among the most promising eco-friendly biological alternatives are plant growth–promoting rhizobacteria (PGPR), including halobacteria, which have significant agricultural potential due to their ability to enhance crop yields and increase plant resistance to various abiotic stresses [10]. Halobacteria are capable of surviving across a broad salinity spectrum (1–25% NaCl) and can also grow in environments lacking NaCl. This adaptability, combined with their plant growth–promoting properties, has led to the proposal of halobacteria as a sustainable option for improving the productivity of salt-sensitive crops and for restoring salinity-degraded soils [11]. In arid environments, microbial metabolic activity is closely linked to soil moisture levels [12], which explains why PGPR adapted to such conditions can endure prolonged drought periods and exert stronger beneficial effects on plants upon rehydration [5,12]. As halobacteria are naturally adapted to the saline conditions typical of arid regions, their use is considered particularly suitable for agricultural applications in these environments [13].

Halobacteria

Extended drought conditions in arid and semi-arid regions, combined with elevated temperatures, high evaporation rates, and increased salt concentrations in soil solutions, impose significant physiological stress on microbial communities [14]. Nevertheless, many microorganisms (including archaea, bacteria, and fungi) have evolved adaptations that enable them to withstand the extreme climatic conditions characteristic of these environments. Salt-tolerant bacteria employ diverse survival strategies that allow them to grow across a broad range of salinity levels. Based on their salinity requirements, these microorganisms are classified as either halotolerant or halophilic. Halotolerant bacteria are capable of surviving in media containing up to 25% NaCl as well as in the absence of NaCl, whereas halophilic bacteria require salt for growth. Halophilic bacteria are further categorized as slightly halophilic, which grow optimally at 1–3% NaCl; moderately halophilic, thriving at 3–15% NaCl; and extremely halophilic, which require salinity levels of 15–25% NaCl [5,15]. The bacterial phyla most frequently detected in saline and xeric soils include Actinobacteria, Bacteroidetes, Firmicutes, Proteobacteria, and Cyanobacteria, with Deinococcus and Verrucomicrobiae occurring at lower abundances. In addition, arid soils also harbor archaeal phyla such as Euryarchaeota, Crenarchaeota, and Thaumarchaeota [16]. Halobacteria encompass a diverse group of halophilic and halotolerant species that have been isolated from saline environments worldwide, spanning a wide range of environmental severity. Roodi et al. [17] reported the isolation of bacterial species belonging to the genera *Halobacillus, Halomonas, Thalassobacillus, Brevibacterium,* and *Bacillus* from saline mine soils in Karak, Pakistan. Similarly, investigations of Romanian salt lakes with salinity levels exceeding 70 g L^{-1} and electrical conductivity values reaching 168.1 dS m^{-1} identified bacterial communities representing three major phyla: *Firmicutes, Proteobacteria,* and *Actinobacteria*. Within *Firmicutes*, genera such as *Bacillus, Virgibacillus, Salinococcus, Marinococcus, Halobacillus, Planococcus, Thalassobacillus,* and *Salimicrobium* were documented. *Halomonas* dominated the *Proteobacteria*, alongside *Vibrio, Idiomarina,* and *Psychrobacter*, while *Nocardiopsis* was the most prevalent genus within *Actinobacteria* [18]. In India's Thar Desert, Sharma et al. [19] isolated bacterial genera including *Bacillus, Corynebacterium, Acinetobacter, Aeromonas,* and *Staphylococcus*. Although many studies have targeted extreme habitats to isolate halobacteria, these microorganisms are widely distributed and can also be found in non-saline environments. For instance, *Micrococcus luteus, Staphylococcus aureus,* and *Staphylococcus lentus* were isolated from freshwater sources such as the Ezzu River in Nigeria [20].

Numerous halotolerant bacteria have been isolated from halophytic plants, suggesting that these plants serve as valuable reservoirs for identifying additional halophytic plant growth–promoting rhizobacteria (PGPR), as plant–microbe associations are already established. Halophytes are plants adapted to saline habitats and are capable of accumulating Na^+ ions in their tissues. However, the hormonal signaling pathways by which halophytic roots sense salt stress and translate this signal into directional growth toward saline zones remain poorly understood [21]. This phenomenon, known as halotropism, is a sodium-specific root growth response [22]. During halotropism, the normal gravitropic response of roots is suppressed, allowing roots to adjust their growth direction to optimize development and survival under high salinity conditions [22].

Several studies have documented halotolerant bacteria associated with halophyte rhizospheres. Mukhtar et al. [23] isolated *Bacillus, Halobacillus,* and *Kocuria* species from the rhizosphere of *Salsola stocksii* and *Atriplex amnicola* in the Kewra salt mines of Pakistan. Ruppel et al. [24] reviewed a wide range of halotolerant bacterial taxa associated with halophytic plants in coastal and arid hypersaline ecosystems. Szymańska et al. [25] reported the isolation of halotolerant endophytic and rhizosphere bacteria from *Aster tripolium*, a halophyte thriving in degraded hypersaline soils. Additionally, halophytic plants of the genus *Suaeda* have been shown to host halotolerant bacteria such as *Bacillus subtilis, Zhihengliuella halotolerans, Erwinia persicina,* and species of *Brachybacterium* and *Brevibacterium* [26].

To persist in high-salinity environments, halobacteria employ two primary adaptive strategies. The first, known as the "salt-in" strategy, involves maintaining elevated intracellular salt concentrations that balance the external environment. The second strategy relies on keeping cytoplasmic salt levels low by counteracting osmotic pressure through the accumulation of compatible solutes [27]. The salt-in mechanism is characteristic of extremely halophilic archaea and anaerobic halophilic bacteria of the order *Halanaerobiales*, where Na^+ ions are actively transported and accumulated within the cell [27]. Nonetheless, variable levels of in vitro Na^+ uptake have also been reported in bacteria from other taxa, including *Vibrio alginolyticus, V. metschnikovii, Flavimonas oryzihabitans,* and *Agrobacterium tumefaciens* [28].

In contrast, the synthesis or uptake of compatible solutes is a widespread adaptive response to both salinity and drought stress. These solutes can be produced internally or imported from the surrounding environment and accumulated in high concentrations without disrupting cellular processes [24]. Compatible solutes enhance membrane fluidity and stabilize proteins by preventing stress-induced denaturation. Common compatible solutes in halophilic and halotolerant microorganisms fall into two major categories: (1) amino acids and their derivatives, including glycine betaine, glutamine, glutamate, proline, and ectoine, and (2) polyols such as sucrose, trehalose, mannosylglycerate, and diglycerol phosphate [29]. Together with salt-in mechanisms, compatible solute accumulation contributes to osmoregulation, supported by additional physiological processes such as Na^+ extrusion via electrogenic Na^+/H^+ antiporters and K^+/Na^+ transporters that promote intracellular K^+ accumulation while reducing Na^+ toxicity [7,27].

Another defining feature of halophilic bacteria is the amino acid composition of their membrane proteins, which are enriched in acidic residues such as glutamate and aspartate and contain fewer basic amino acids like lysine and arginine. This negatively charged protein composition helps maintain membrane stability under high intracellular salt conditions and facilitates water retention, thereby supporting enzymatic activity [24,27]. Many halotolerant bacteria also produce exopolysaccharides (EPS) that form biofilms, enhancing moisture retention and creating a hydrated microenvironment while limiting salt penetration into the cell [11]. Bacterial EPS consist of homo- or heteropolysaccharides composed of monosaccharides such as glucose, galactose, and mannose, along with neutral sugars (e.g., rhamnose and fucose), uronic acids (glucuronic and galacturonic acids), amino sugars, and various organic substituents [30]. EPS composition varies among species and is influenced by growth stage, nutrient availability, and environmental conditions [30]. Several rhizosphere-associated bacterial genera, including *Enterobacter, Aeromonas, Bacillus, Planococcus, Halomonas, Burkholderia, Microbacterium,* and *Paenibacillus*, are known EPS producers and biofilm formers [5]. Nearly all species of the genus *Pseudomonas* synthesize alginate—an EPS composed of D-mannuronic and L-glucuronic acids—although its composition can shift under stress conditions. For example, *Pseudomonas* spp. GAP-45 altered alginate composition when exposed to elevated temperature, salinity, and desiccation stress [31,32].

Plant Growth-Promoting Halobacteria and Protection against Abiotic Stress

Plant growth–promoting rhizobacteria (PGPR) are soil-dwelling bacteria that colonize the rhizosphere and enhance plant development through a range of direct and indirect mechanisms. Direct modes of action include biological nitrogen fixation, synthesis of phytohormones, production of the enzyme 1-aminocyclopropane-1-carboxylate (ACC) deaminase, solubilization of phosphorus and potassium, and secretion of siderophores that facilitate iron acquisition. Indirect mechanisms involve the induction of systemic resistance in plants and the release of antimicrobial substances that suppress phytopathogens [33,34]. Halobacteria also exhibit both direct and indirect plant growth–promoting traits, enabling them to support plant development even under highly saline conditions [2]. The beneficial effects of halotolerant and halophilic bacteria on plant growth have been widely reported [5,35–37] and are mediated through several mechanisms, including:

1. **Activation of plant antioxidant defense systems** by modulating enzymes such as superoxide dismutase, peroxidase, and catalase, which detoxify reactive oxygen species and alleviate salinity-induced oxidative stress.

2. **Enhancement of plant nutrient availability** through atmospheric nitrogen fixation, solubilization of essential nutrients such as phosphorus and potassium, and siderophore production that improves iron uptake.
3. **Regulation of ion homeostasis** by promoting selective ion absorption to maintain a favorable K^+/Na^+ ratio, thereby limiting the buildup of harmful ions such as Na^+ and Cl^-.
4. **Reduction of sodium accumulation in plants** via the secretion of exopolysaccharides that bind Na^+ in the rhizosphere, restricting its movement to aerial tissues; these exopolysaccharides also contribute to improved soil aggregation and structure.
5. **Lowering plant ethylene levels** through ACC-deaminase activity, which alleviates stress-induced growth inhibition.
6. **Alteration of root architecture and morphology**, enhancing water and nutrient uptake; as noted by Szepesi [21], halotropism enables roots to adjust growth patterns and structure efficiently to cope with high salinity.
7. **Accumulation of osmoprotective compounds**, including amino acids (e.g., glutamate and proline), amines (e.g., carnitine, glycine, and betaine), and sugars (e.g., sucrose and trehalose), which help mitigate intracellular osmotic stress.
8. **Improvement of stomatal conductance and photosynthetic performance**, supporting overall plant productivity.
9. **Induction and regulation of stress-responsive gene expression** in plants, strengthening tolerance to adverse environmental conditions.

Effect of Halobacteria on Soil Fertility

The majority of research on halobacteria has primarily concentrated on their ability to enhance plant growth and crop productivity under saline conditions, and to a lesser extent under other abiotic stresses such as drought [39] and heavy metal toxicity [38,40,41,42]. Consequently, the influence of halobacteria on soil fertility has not been extensively examined. Nevertheless, some studies have reported improvements in soil structure and fertility following inoculation with halobacteria [11]. The application of these microorganisms has been shown to significantly enhance the availability of essential nutrients, including nitrogen, phosphorus, potassium, and iron, often without causing substantial alterations to the native soil microbial community [43]. Several bacterial genera—such as *Azospirillum, Alcaligenes, Bacillus, Burkholderia, Enterobacter, Flavobacterium, Pseudomonas,* and *Rhizobium*—have demonstrated the capacity to mitigate the adverse effects of salinity on crops while simultaneously improving soil organic matter content, structure, and water-holding capacity [11].

Mukhtar et al. [23] investigated the growth of maize inoculated with *Bacillus safensis, B. pumilus, Kocuria rosea, Enterobacter aerogenes,* and *Aeromonas veronii* under saline stress. These halobacteria, isolated from the rhizosphere of halophytic plants, exhibited phosphate-solubilizing activity. In addition to promoting maize growth, their inoculation significantly increased phosphorus availability in the soil. Similarly, Pankaj et al. [44] evaluated the effectiveness of *Pseudomonas plecoglossicida* (KM233646), *Acinetobacter calcoaceticus* (KM233647), *Bacillus flexus* (KM233648), and *B. safensis* (KM233652) in enhancing the growth and yield of *Bacopa monnieri* (L.), a plant known for its ability to accumulate Na^+ and K^+ in saline soils. Soils treated with halobacteria showed elevated activities of dehydrogenase, alkaline phosphatase, and acid phosphatase, along with increased total nitrogen, organic carbon, and available phosphorus compared to non-inoculated controls. In contrast, parameters such as the Na^+/K^+ ratio, electrical conductivity, pH, exchangeable sodium percentage, and Na^+ uptake rate were reduced in inoculated soils.

Al-Enazy et al. [45] demonstrated that inoculating maize with *Azotobacter chroocococcum, Bacillus megaterium,* and *Pseudomonas fluorescens*, combined with the application of phosphogypsum to saline soils in Saudi Arabia, resulted in significant reductions in soil electrical conductivity and pH. Hassan et al. [46] assessed the impact of powdered roots of a halophytic plant containing three halotolerant bacteria (*Bacillus cereus, Pseudomonas moraviensis,* and *Stenotrophomonas maltophilia*) on wheat growth and soil fertility. Their results showed marked decreases in soil electrical conductivity and Na^+ uptake, accompanied by increases in potassium, phosphorus, and nitrate concentrations following inoculation.

Anees et al. [47] examined the combined inoculation of halotolerant bacteria (*Pseudomonas, Thalassobacillus,* and *Terribacillus* spp.) with chitinolytic bacteria (*Pseudomonas* spp. Fo1, *Sanguibacter* spp. Ft2, *Bacillus* spp. Ft4, and *Bacillus* spp. Fc3) in spinach (*Spinacia oleracea* L.). Their findings revealed a substantial reduction in soil electrical conductivity from 6.5 to 2 dS m^{-1} and a decrease in Na^+ concentration from 22–24 to 9–12 meq L^{-1} after harvest. Additionally, root and shoot dry biomass increased, while the leaf Na^+/K^+ ratio declined. Arora [48] reported notable improvements in soil pH (from 9.42 to 8.91) and a reduction in exchangeable sodium content (from 416 to 238 mg kg^{-1}) following two years of continuous inoculation of rice and wheat with commercial bioinoculants derived from PGPR isolated from halophytic plants. These treatments also led to increased soil microbial biomass carbon and enhanced dehydrogenase activity compared with uninoculated soils.

Overall, these findings suggest that halobacterial inoculation not only promotes plant growth but also plays a significant role in restoring key soil fertility parameters, offering a dual advantage of enhanced crop productivity and improved soil health.

Conclusion

Halobacteria are microorganisms that are well adapted to harsh environmental conditions due to specialized physiological mechanisms that enable them to withstand varying salt concentrations. They are widely distributed across diverse ecosystems. These bacteria promote plant growth through a range of direct and indirect pathways, leading to improvements in plant biometric and physiological traits as well as enhanced yields in several salt-sensitive crops. Research on halobacteria has predominantly emphasized their role in improving plant growth and productivity under saline conditions, with comparatively fewer studies examining their effects under other stresses such as drought and heavy metal contamination. As a result, their influence on soil fertility remains insufficiently explored. Incorporating soil fertility assessments into halobacterial research, along with the use of quantitative criteria for selecting effective strains, could improve our understanding of their impact on soil properties and support the restoration of arid and semi-arid soils that have been degraded by salinity and drought.

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