REVIEW ARTICLE

Harnessing Rhizospheric Microbes for Eco‑friendly and Sustainable Crop Production in Saline Environments

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Abstract

Soil salinization is a global issue that negatively impacts crop yield and has become a prime concern for researchers worldwide. Many important crop plants are susceptible to salinity-induced stresses, including ionic and osmotic stress. Approximately, 20% of the world's cultivated and 33% of irrigated land is afected by salt. While various agricultural practices have been successful in alleviating salinity stress, they can be costly and not environment-friendly. Therefore, there is a need for cost-efective and eco-friendly practices to improve soil health. One promising approach involves utilizing microbes found in the vicinity of plant roots to mitigate the efects of salinity stress and enhance plant growth as well as crop yield. By exploiting the salinity tolerance of plants and their associated rhizospheric microorganisms, which have plant growth-promoting properties, it is possible to reduce the adverse efects of salt stress on crop plants. The soil salinization is a common problem in the world, due to which we are unable to use the saline land. To make proper use of this land for diferent crops, microorganisms can play an important role. Looking at the increasing population of the world, this will be an appreciated efort to make the best use of the wasted land for food security. The updated information on this issue is needed. In this context, this article provides a concise review of the latest research on the use of salt-tolerant rhizospheric microorganisms to mitigate salinity stress in crop plants.

Abbreviations

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Introduction

The rapid growth of the world's population has made it imperative to boost the production of crucial crop plants by expanding cultivation areas, including those afected by salinity and degraded land. About a 50% increase in grain yield of rice, wheat and maize will be required to feed the projected population by 2050 [\[1](#page-10-0)]. Seven million hectares of land are affected by salinity in India [\[2](#page-10-1)]. Salt stress is one of the key factors accountable for the losses in crop yield. Low rainfall and rock weathering are increasing salinity at the rate of 10% annually. According to Ouhibi et al. [[3](#page-10-2)], salinity has increased due to inappropriate use of nutrients, inadequate irrigation and pollution. Elevated concentrations of sodium and chlorine ions in the soil lead to soil salinity, which further develops hyperosmotic conditions. Jamil et al. [\[4](#page-10-3)], predicted that $>50\%$ of the arable land may be salinized by 2050. Krasensky and Jonak [[5\]](#page-10-4), reported that high soil salinity creates an imbalance in the cellular osmotic potential inside the cell. Salt-stressed soils reduce the development of plants [[6\]](#page-10-5). Soil salinity decreases the rate of nutrient uptake [\[7](#page-10-6)]. Many crop plants are glycophytes, which are salt sensitive and their growth is adversely afected by salt stress [\[8](#page-10-7)]. Wang et al. [[9](#page-10-8)] showed the role of microbial communities in long-term phytoremediation of coastal saline soil. They observed that the microbial community was plant speciesspecifc. Overall abiotic stresses cause adverse efects on plant growth [[10](#page-10-9)]. Globally, soil salinization is a menace to agricultural productivity [[11\]](#page-10-10).

The rhizosphere is a soil region in the vicinity of plant roots. This soil harbours many bacteria, fungi, cyanobacteria, etc. which interact with the plants and induce positive, negative or neutral efects on the host. The rhizosphere covers an area of a few millimetres in the surrounding of the plant root. The plants sufer from diferent types of stresses that can be broadly classifed as biotic and abiotic categories. Biotic stresses in crop plants encompass the impacts of fungi, bacteria, viruses, protozoa, nematodes, algae, and parasitic plants. Meanwhile, abiotic stresses in crop plants are attributed to factors such as soil and water salinity, inadequate moisture levels, extreme temperatures, and nutrient excesses or defciencies. Hence, new technologies and methods are required to improve soil health through plant–microbe interactions [[12\]](#page-10-11).

In the natural environment, plants are colonized by diverse microbial communities [[13\]](#page-10-12). Among these, benefcial rhizospheric microorganisms have been shown to enhance plant health and performance under unfavourable environmental conditions, ultimately leading to increased crop productivity [\[14\]](#page-10-13). Plant growth-promoting bacteria (PGPB) are known to stimulate plant growth and development by providing essential nutrients [[15\]](#page-10-14). In particular, salttolerant and plant growth-promoting microbes offer a promising avenue for the management of salt stress in various crop plants. This work aims to compile the latest research in salt stress management to increase the food grain production that is hampered heavily by saline land. Microorganisms can alleviate and revive the saline soil for the potential production of food grains from diferent crops.

Adverse Efects of Soil Salinity on Plants

Soil salinization poses a signifcant threat to agriculture and is a big challenge in crop production [[11\]](#page-10-10). When crops are grown in saline soils, they often fail to reach their genetic potential and yield reduction is common [\[4](#page-10-3), [16\]](#page-10-15). Based on electrical conductivity (EC) values, soils can be classifed into seven categories ranging from non-saline $(0-2 dS m^{-1})$ to extremely saline (> 32 dS m⁻¹), as proposed by Rasool et al. [[17\]](#page-10-16). Soil salinization occurs across all climates and altitudes, including in desert regions [[18\]](#page-10-17). Salts are ubiquitous in both soil and water. Even high-quality canal and groundwater sources used for irrigation contain dissolved salts. These salts are essential for plant growth, but excessive accumulation can result in soil salinization caused by mineral weathering, inorganic fertilizer use, and irrigation water [[19\]](#page-10-18). Salinity is increased by crop irrigation and it introduces salinity including new salts to the soils [[20](#page-10-19)]. About 2% of dry-land agriculture, and>45 Mha of irrigated land have been badly affected by salinity [[21\]](#page-10-20). Salinity problems resulting from seawater and saline water irrigation are prevalent in Mediterranean regions [\[22](#page-11-0)], while in Australia, oceanic salt deposition is a major contributor to soil salinity [[23\]](#page-11-1). Any soluble material added to the soil can increase its salinity level [[18](#page-10-17)]. Poor drainage in irrigated agricultural lands is a serious concern that may lead to soil salinization and conversion of productive agricultural lands into saline lands [\[24](#page-11-2), [25](#page-11-3)]. Effective management of soil salinity is crucial to prevent soil sodicity, which can compromise soil tex-ture and structure [[18\]](#page-10-17).

Soil salinity causes ion toxicity, nutrient deficiency, osmotic and oxidative stress on plants, and thus restricts water uptake [[26\]](#page-11-4). The yield and productivity of crops are hampered to a great extent by soil salinity [[23,](#page-11-1) [27,](#page-11-5) [28\]](#page-11-6). Soil salinity adversely affects seed germination, photosynthesis, plant growth and uptake of nutrients and water [[18,](#page-10-17) [29](#page-11-7)]. Salinity stress causes a reduction in the photosynthetic rate in crops like sugarcane It is a response against stress in which moisture loss is reduced through the partial closure of stomata, stomatal conductance reduction, reduced transpiration, and, then, limitation in the internal stomatal $CO₂$ concentration [[30\]](#page-11-8). There is minimal adverse effect on the crop yield at low salt concentrations [[31\]](#page-11-9). However, in saline conditions, crop production decreases because plants are unable to grow at high salt concentrations (100–200 mM NaCl) and afected plants may die. This is because plants evolved under low saline conditions do not exhibit salt tolerance $[32]$ $[32]$ $[32]$. Soil salinity affects plant photosynthesis by reducing leaf area and chlorophyll content and alters many other plant growth processes [[33](#page-11-11)]. Reproductive growth is also afected by salinized soil. On the other hand, halophytes can survive in high saline conditions $(>300-400 \text{ mM})$. Halophytes can live under saline conditions due to their ability to adapt to saline soil as they have developed salt tolerance mechanisms. High salinity hampers the ability of roots to absorb water. Moreover, high salt within the plant may be toxic, which further interferes with many essential plant biological processes [[23,](#page-11-1) [34–](#page-11-12)[36\]](#page-11-13).

Microbial Diversity in the Rhizosphere

Rhizosphere, the region of soil surrounding plant roots, is a dynamic and complex environment that is heavily infuenced by the activity of diverse microbial communities [[37](#page-11-14)]. In the context of salinity stress, the rhizosphere is of particular interest due to the role of microbes in mitigating the negative efects of high soil salinity on plant growth and productivity. Research on microbial diversity in the rhizosphere has revealed that salinity stress can infuence the composition and function of microbial communities in this environment [\[38](#page-11-15)]. For example, studies have shown that high salinity levels can lead to changes in microbial community structure, with shifts towards halophilic (salt-tolerant) bacterial and fungal taxa, as well as changes in the relative abundance of diferent microbial functional groups (e.g., nitrogen-fxing bacteria, phosphate-solubilizing bacteria). In addition to shifts in microbial community structure, research has also demonstrated that specifc microbial taxa and functional groups may play important roles in mitigating the negative efects of salinity stress on plants. For example, some halophilic bacterial and fungal species have been shown to produce compounds that help to protect plant cells from damage caused by high salt concentrations. Other microbial species may enhance plant tolerance to salinity stress by facilitating nutrient uptake or producing plant growth-promoting substances [\[39](#page-11-16)].

The research on microbial diversity in the rhizosphere highlights the potential for harnessing the power of microbes to manage crop salinity stress [[40](#page-11-17)]. By understanding the complex interactions between plants and the diverse microbial communities in the rhizosphere, researchers and farmers may be able to develop innovative microbial solutions that improve crop productivity and resilience in the face of salinity stress.

Mechanisms of "Microbial Salinity Tolerance" and Plant Growth Promotion

Microbes that are adapted to saline environments are known to possess various mechanisms that allow them to tolerate high salt concentrations. These mechanisms (Fig. [1](#page-3-0)) include the production of compatible solutes, the activation of specifc transport systems for ions and water, and the synthesis of extracellular polysaccharides that can act as a protective barrier against salt stress. For example, halophilic bacteria such as *Halomonas* and *Salinivibrio* produce high levels of compatible solutes such as glycine betaine and trehalose, which help to maintain cellular homeostasis under high salt concentrations. In addition, some microbes can modulate the plant's response to salt stress by inducing the expression of stress-responsive genes or by producing phytohormones that promote plant growth and development. Plant growth-promoting microbes (PGPMs) can also enhance plant growth and productivity under saline conditions through various mechanisms. For instance, PGPMs can produce plant growth-promoting substances such as indole acetic acid (IAA), gibberellins, and cytokinins, which stimulate plant growth and development [\[41,](#page-11-18) [42](#page-11-19)]. They can also enhance nutrients uptake by solubilizing insoluble nutrients such as phosphorus and iron or by fxing atmospheric nitrogen. Moreover, PGPMs can reduce the negative impact of salt stress on plant growth by lowering the concentration of toxic ions such as sodium (Na^+) and chloride (Cl^-) in the plant tissue. In addition to the above mechanisms, microbes can also interact with each other to form complex microbial communities in the rhizosphere, which can enhance plant growth and productivity under heavy metal toxic conditions [[43](#page-11-20)]. These communities can form bioflms that protect the microbes from salt stress, facilitate nutrient exchange between diferent microbial species, and enhance the production of plant growth-promoting substances.

In plants, many genes control the salinity tolerance in plants. We can measure the genetic variation indirectly by observing the response of diferent genotypes [\[44\]](#page-11-21). During the process of evolution, plants have evolved three mechanisms to adapt to salinity. Organic ions (K^+, Cl^{-}) and osmolytes such as proline, glycine, betaine and soluble sugars help in maintaining osmoregulation, which is essential to maintain the turgidity of plant cells. Proline maintains the osmotic stability of the plant cells and protects them from salt injury. Proline concentration increases under the infuence of certain microbes, which further helps in the alleviation of salt stress in plants. Betaines are ammonium compounds that plants produce under salt stress. Phytohormones **Fig. 1** Alleviation of salt stress in plants by rhizospheric microorganisms using diferent salt tolerance mechanisms including an increase in production of IAA, CAT, SOD, POX, ACC deaminase activity, total soluble sugars, osmoprotectants, betaine proline, antioxidant enzyme and EPS and decrease in reactive oxygen spp.

such as strigolactones, jasmonic acid (JA) and abscisic acid (ABA) play important roles in plant growth and salinity management. Ionic homeostasis in plant cells is also very important for normal growth in plants. The antioxidant defense mechanisms have an important role in inhibiting salinity stress and enhancing crop growth [[45\]](#page-11-22). The enzymatic antioxidants include catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), ascorbate peroxidase (APX), guaiacol peroxidase (GPX) and glutathione reductase (GR), while non-enzymatic antioxidants are ascorbate (AsA), carotenoids, glutathione and phenolics.

Microbial Solutions for Alleviating Crop Salinity Stress

Microbial solutions for managing crop salinity stress have several advantages over conventional practices. Microbial treatments are cost-efective, environmentally friendly, and sustainable. These solutions do not contribute to soil degradation or pollution, and imply that the organisms reduce the need for fertilizers and chemical pesticides. Moreover, microbial treatments have been shown to enhance soil health, increase nutrient availability, and improve plant growth and stress tolerance (Fig. [2\)](#page-4-0). Many research works found that the use of PGPB is a reliable option to reduce plant stress caused by salinized soil [[46](#page-11-23)]. These salts are essential for plant growth, but excessive accumulation can result in soil salinization caused by mineral weathering, inorganic fertilizer use, and irrigation water [[19](#page-10-18)]. Microbial amelioration of crop salinity stress, induction of abiotic stress tolerance in plants by endophytic microbes and role of salt tolerant plant growth promoting rhizobacteria for enhancing crop productivity of saline soils have been reviewed [[47](#page-11-24)[–49](#page-11-25)]. Salinity stresses induced physio-biochemical changes in sugarcane and its tolerance mechanism and mitigating approaches have been recently reviewed by Kumar et al. [\[50\]](#page-11-26). Salt-tolerant arbuscular mycorrhizal fungi (AMF), cyanobacteria, endophytes, fungi and bacteria are highly efective in salt stress amelioration in plants and are discussed here.

Arbuscular Mycorrhizal Fungus (AMF)

Numerous studies have demonstrated the efectiveness of arbuscular mycorrhizal fungi (AMF) in managing salinity stress in various crops. For example, Tisarum et al. [[51](#page-11-27)], showed that the AMF *Glomus etunicatum* can mitigate the adverse efects of salinity on rice by increasing fructose and free proline. In addition, the AMF *Funneliformis mosseae* has been shown to reduce salt stress in pigeon peas [\[52](#page-11-28)] and soybean [[53\]](#page-11-29) by enhancing the activity of catalase (CAT),

Fig. 2 Illustrations show salt stress alleviation from soil and water using prominent microorganisms' genera i.e. *Halomonas, Bacillus*, *Sphingobacterium*, *Staphylococcus*, *Pseudomonas*, *Serratia*, *Arthrobacter*, *Enterobacter*, *Micrococcus*, *Planococcus*, and *Variovorax* spp.

superoxide dismutase (SOD), and peroxidase (POX). Furthermore, a mixture of Glomus fungi (AMF) was found to decrease soil salinity efects by increasing CAT and POX enzymes in wheat crops [\[54](#page-11-30)].

Cyanobacteria

Cyanobacteria have been identifed as a potential solution to mitigate the harmful effects of salinity stress on crops. Several studies have reported that cyanobacteria employ various mechanisms to alleviate salt stress. For instance, *Synechococcus elongatus* PCC 7942, a type of cyanobacterium, accumulates sucrose as a compatible solute to manage salt stress [[55\]](#page-11-31). Similarly, another cyanobacterium, *Synechococcus elongatus* UTEX 2973, synthesizes sucrose as an osmoprotectant to mitigate the negative impact of salinity [\[56](#page-11-32)]. These fndings suggest that cyanobacteria could be a potential microbial solution for alleviating crop salinity stress.

Endophytes

Endophytes are an important group of bacteria or fungi which live inside the host plants asymptomatically without causing any harm to the plants. These endophytes take nutrients and shelter from the plants for their survival. In return, endophytes help in the alleviation of many abiotic stresses viz. salt stress, drought stress, heat stress metal toxicity etc. faced by the plant under diferent soil and environmental conditions. Endophytes also make the required nutrients available to the plants. Endophyte strains *Pseudomonas pseudo alcaligenes* + *Bacillus pumilus* + *Achromobacter xylosoxidans* UM54 alleviated the efect of salinity in rice crops by causing a reduction in lipid peroxidation and superoxide dismutase activity [[57\]](#page-11-33). Similarly, *Pantoea indica* also ameliorates the salinity effect in rice by increasing the glycerol concentration [\[58](#page-12-0)]. Detailed reviews on the importance of endophytes in mitigating abiotic stresses in plants have been given by various workers [[48,](#page-11-34) [59,](#page-12-1) [60\]](#page-12-2).

Fungi

Fungi also play a vital role in salt stress management in various crops by the production of diferent types of compounds [[61\]](#page-12-3). In a study conducted by Ripa et al. [[62\]](#page-12-4), it was found that *Trichoderma aureoviride* and *T. harzianum* fungi are efective in mitigating the harmful efects of salinity on wheat crops by enhancing the production of indole acetic acid (IAA) and though phosphorus solubilisation. The use of *Trichoderma longibrachiatum* T6 also resulted in a signifcant reduction in salt stress in wheat through the production of IAA and ACC-deaminase, which in turn improved crop productivity [[63\]](#page-12-5). Furthermore, Kashyap et al. [\[64](#page-12-6)], demonstrated that the application of salt-tolerant *Trichoderma* and *Hypocrea* fungi could be a potential biological strategy to manage *Rhizoctonia solani* AG-4, which causes tomato root rot under saline conditions. These fndings highlight the potential of using *Trichoderma* fungi as a microbial solution for alleviating crop salinity stress and enhancing plant growth.

Bacteria

Bacteria have been shown to have great potential for the bio-remediation of saline soils, as highlighted by Arora et al. [\[65](#page-12-7)], which can lead to enhanced agricultural production. The rhizospheric soil is a rich source of bacteria, and researchers have identifed many bacteria and plant growthpromoting rhizobacteria (PGPR) that are tolerant to various abiotic stresses such as drought, heat, and salinity. These stress-tolerant bacteria have been used to alleviate and manage diferent types of abiotic stresses in many economically important crop plants. The consortium of rhizospheric microorganisms: *Brevibacillus fuminis*, *Brevibacillus agri* and *Bacillus paralicheniformis* has been efective in salt stress amelioration in solanaceous crops [\[66\]](#page-12-8). The consortium bacteria increased the production of indole-3-acetic acid (IAA) and ammonia. They are also helpful in Zn and P solubilisation. *Bacillus amyloliquefaciens* NBRISN13 (SN13) strain has been found to alleviate salt stress in rice crops [\[67](#page-12-9)]. Kumar et al. [\[68](#page-12-10)], showed the potential of PGPR in salt stress management in medicinal plants. Saghaf et al. [\[69](#page-12-11)], gave a detailed account of the increase in rapeseed crop production in saline soils using salt-tolerant PGPRs. It was observed that PGPRs increase ACC deaminase, IAA production and phosphate solubilisation. Yasin et al. [\[70](#page-12-12)], observed the important role of halotolerant PGPRs and kinetin in the amelioration of salt stress in black gram. It was reported that improvement in H_2O , photosynthesis and gas exchange mitigated the efect of salinity in this case.

It is clear from the literature that a variety of salt-tolerant rhizospheric microbes have been identifed and studied for their role in alleviating the harmful efects of salinity on crop plants. Bacteria such as *Halomonas*, *Bacillus*, *Sphingobacterium*, *Staphylococcus*, *Pseudomonas*, *Serratia*, and *Arthrobacter* are effective in controlling salinity in various crop plants by inducing antioxidant systems, osmoregulation, nutrient uptake, and hormone production. These bacteria also help in maintaining ionic balance and homeostasis in plants to mitigate the harmful efects of salinity. In addition, these bacteria produce hydrolytic enzymes, siderophores, and solubilize phosphates to enhance nutrient uptake by the plants. In addition, some bacteria augment the levels of compatible solutes such as glycine betaine and proline, and antioxidant enzymes like CAT, SOD, and POD, to protect the plants from salinity stress. Furthermore, some bacteria also fx atmospheric nitrogen and produce ACC deaminase, which reduces the ethylene levels in plants and further improves their tolerance to salinity stress. Overall, the use of salt-tolerant rhizospheric microbes can be a promising

strategy for the management of salinity stress in various crop plants. Detailed information on microorganisms and their role in alleviating salt stress is given in Table [1](#page-6-0).

Challenges in Microbial Solutions for Crop Salinity Stress

Crop salinity stress is a major concern for agricultural productivity worldwide. The use of microbial solutions has emerged as a promising approach for mitigating the harmful efects of salinity on crops. Despite the encouraging results from various studies, there are still some challenges that need to be addressed to further enhance the efficacy and applicability of microbial solutions in crop salinity stress. One of the major challenges is the variability in the efficacy of microbial solutions across diferent crops and environments. The efectiveness of microbial solutions depends on a variety of factors such as the type of crop, soil type, climatic conditions, and the specifc microbial strains used. Therefore, more research is needed to identify the most suitable microbial strains for diferent crops and environments and to optimize the conditions for their application. Another challenge is the lack of understanding of the mechanisms by which microbial solutions alleviate crop salinity stress. Although several studies have demonstrated the benefcial efects of microbial solutions on crop growth and productivity under saline conditions, the exact mechanisms by which they work are still not fully understood. More research is needed to elucidate the specifc biochemical pathways and molecular mechanisms involved in microbial-mediated salinity stress alleviation. Furthermore, the scalability and cost-efectiveness of microbial solutions for large-scale agricultural applications remain a challenge. The development of cost-effective and efficient methods for large-scale production and application of microbial solutions is crucial for their widespread adoption in agriculture. In addition, the development of standardized protocols for the preparation, application, and monitoring of microbial solutions is needed to ensure consistent and reliable results across diferent locations and crops. Lastly, there is a need for more extensive field trials and demonstrations to validate the efficacy of microbial solutions in real-world agricultural settings. Many of the studies conducted so far have been in controlled laboratory or greenhouse conditions, and their efficacy under feld conditions needs to be further validated.

Conclusions

In conclusion, microbial products have immense potential in mitigating the adverse efects of salinity stress in crop plants. Numerous studies have reported the efectiveness

Table 1 (continued)

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*-:Not given/not available *-:Not given/not available

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Table 1 (continued)

of various microorganisms, including bacteria, fungi, and algae, in improving crop growth and yield under salinity stress conditions. Microbial solutions offer several advantages over conventional methods of salinity stress management, such as cost-efectiveness, environmental safety, and sustainability. However, several challenges need to be addressed to realize the full potential of microbial solutions for crop salinity stress.

Future Plan

There is a need for a better understanding of the mechanisms by which microorganisms alleviate salinity stress in plants. This will help in the development of more efficient microbial solutions for salinity stress management. There is also a need to identify and characterize more efective and specifc microbial strains that can tolerate and mitigate the adverse efects of high salt concentrations in the soil. The formulation and delivery of microbial solutions for salinity stress management need to be optimized. This includes developing methods for mass production, storage, and application of microbial products and there is a need to establish regulatory frameworks and guidelines for the use of microbial solutions in agriculture to ensure their safety and efficacy. Microbial solutions offer a promising and sustainable approach to managing crop salinity stress, with continued research and development, microbial solutions have the potential to play a signifcant role in ensuring food security and sustainable agriculture in regions afected by salinity stress.

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Declarations

Conflict of interest The authors declare that there is no confict of interest.

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