Plant growth promoting bacteria as a tool to mitigate salt stress in crops: A review

Bacterias promotoras de crecimiento vegetal como una herramienta para mitigar el estrés salino en cultivos: una revisión

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ABSTRACT

Salinity is a factor that negatively affects the physiology of most plants, even placing food security at risk when it affects plants grown for food. This review provides an overview of the use of plant growth-promoting bacteria (PGPB) as a strategy for enhancing crop growth under salt stress, aiming to provide a sustainable solution for this environmental problem. Salinity causes morphophysiological and biochemical alterations in plants due to osmotic and ionic stress. Plants have different response mechanisms that allow them to survive and, in some cases, tolerate salinity. Various mitigation strategies have been evaluated, such as the use of plant hormones, fertilizers, nanofertilizers, silicon, antioxidants, tolerant genotypes, and inoculation with microorganisms, among others. Among the organisms used for inoculation, PGPB are of particular interest. PGPB, with the capacity to tolerate salinity conditions, can enhance germination, seedling vigor, root and shoot growth, and chlorophyll content in plants, in addition to other positive impacts. The mechanisms of action of PGPBs have been extensively studied and used to improve the quality of commercial crops and to produce bioinoculants. The study of these microorganisms is ongoing; more knowledge is needed on the mechanisms of action of the bacteria, the mechanisms of colonization, and the genes involved in the mechanisms of promotion and colonization. Additionally, it is necessary to expand knowledge of the most efficient ways to use these organisms in crops of commercial and environmental interest.

Key words: PGP bacteria, inoculation, biofertilizers, salinity, halotolerant rhizobacteria, abiotic stress.

RESUMEN

La salinidad es un factor que afecta negativamente la fisiología de la mayoría de las plantas, llegando incluso a poner en riesgo la seguridad alimentaria cuando afecta a las plantas cultivadas para producir alimentos. Esta revisión provee una descripción general del uso de las bacterias promotoras del crecimiento vegetal (BPCV) como una estrategia para mitigar el estrés salino en plantas, con una mirada para proveer una solución sustentable a este problema ambiental. La salinidad provoca alteraciones morfofisiológicas y bioquímicas en plantas debido al estrés osmótico e iónico. Las plantas tienen diferentes mecanismos de respuesta que les permiten sobrevivir y en algunos casos tolerar la salinidad. Se han evaluado diferentes estrategias de mitigación, como el uso de hormonas vegetales, fertilizantes, nanofertilizantes, silicio, antioxidantes, genotipos tolerantes e inoculación con microorganismos, entre otros. Entre los microorganismos utilizados para la inoculación, son de particular interés las BPCV. Las BPCV con capacidad de tolerar condiciones de salinidad pueden mejorar los procesos de germinación, el vigor de las plántulas, el crecimiento de raíces y brotes y el contenido de clorofila en las plantas, además de otros impactos positivos. Los mecanismos de acción de las BPCV han sido ampliamente estudiados y utilizados para mejorar la calidad de los cultivos comerciales y para la producción de bioinoculantes. El estudio de estos microorganismos está en curso. Se necesita más conocimiento sobre los mecanismos de acción de las bacterias, los mecanismos de colonización y los genes involucrados en los mecanismos de promoción y colonización. Además, es necesario ampliar el conocimiento sobre la forma más eficiente de utilizar estos organismos en cultivos de interés comercial y ambiental.

Palabras clave: BPCV, inoculación, biofertilizantes, salinidad, rizobacterias halotolerantes, estrés abiótico.

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Introduction

The decrease in crop yield and quality worldwide is due to biotic and abiotic stress. Salinity is among the primary factors that induce abiotic stress in plants. It is considered one of the most significant environmental problems in the world, posing a threat to food security (Ibrahimova *et al*., 2021) and jeopardizing the achievement of the Sustainable Development Goals. Statistics indicate that saline soils represent more than 6% of the total land area and approximately 20% of the total cultivated area globally; the latter percentage could increase to 50% by 2050 (Bullaín Galardis *et al*., 2022). With significant economic loss, Qadir *et al.* (2014) estimated that salt-affected irrigated lands result in annual income losses of approximately USD 27.3 billion (adjusted for inflation) due to reductions in crop yields.

Salinity is considered an excess of soluble salts present in the soil (Ansari *et al*., 2022). This excess is due to natural causes in areas with arid and semi-arid soils, as well as anthropogenic factors (Bullaín Galardis *et al*., 2022), including poor irrigation practices in agricultural areas and increased evaporation during drought due to climate change (Van Zelm *et al*., 2020).

Plants under salinity conditions present morphophysiological and biochemical alterations due to osmotic and ionic stress (Safdar *et al*., 2019). The production of reactive oxygen species causes membrane damage, a decrease in photosynthesis, nutrient imbalance, changes in hormone concentrations, enzyme inactivation, and metabolic dysfunction (Fu & Yang, 2023; Negrão *et al*., 2017) resulting in decreased growth and crop production.

There are halophytic species that can tolerate high levels of salinity. But most cultivable plants are glycophytes, which are very sensitive to salt stress. These plants present various mechanisms at the physiological, biochemical, and molecular levels in response to stress (Acosta-Motos *et al*., 2017; Ismail & Horie, 2017). However, in severe cases of salinity stress, defense mechanisms are compromised, and plants suffer the effects of stress (Nigam *et al*., 2022). Nonetheless, several management strategies can help mitigate salinity damage, including genetic improvement, the use of organic and inorganic amendments, fertilization management, the presence of mycorrhizae, the application of antioxidant substances, and growth regulators, among others. Additionally, the use of plant growth-promoting bacteria (PGPB) is a promising strategy.

PGPBs have been evaluated for mitigating different biotic and abiotic stresses. The role of PGPB in inducing tolerance to salt stress through the provision of various nutrients, conservation of a high K^+/Na^+ ratio, increased osmolyte accumulation, increased photosynthetic rates and biomass, and the activity of antioxidant enzymes have been reported in different crops (Bhise & Dandge, 2019; Kushwaha *et al*., 2020; Nigam *et al*., 2022). These include leguminous (Khan & Basha, 2015), lettuce (Fasciglione *et al*., 2015), wheat (Ramadoss *et al*., 2013) among others. The issue of salt stress in crops represents a significant challenge for global agricultural production. Various approaches have been explored to mitigate its effects, including the use of PGPB. However, it is essential to establish a clear connection between salt stress and the functionality of these bacteria, allowing for a better understanding of their mechanisms of action and their applicability in different agricultural contexts. This review provides an overview of the use of PGPB as an alleviation strategy for crop plants under salt stress, deepening the understanding mechanism of the mechanism at the molecular, biochemical, and physiological levels to provide a sustainable and practical solution for this environmental problem. Aspects related to the main bacterial strains, inoculants, and biotechnology processes are included.

Effects of salt stress on plant physiology

The adverse effects of salt stress in reducing plant growth and productivity have two leading causes according to Ismail and Horie (2017). The first of these is osmotic stress, which reduces water uptake by the roots, resulting in effects similar to those caused by water deficit. The second cause is the direct accumulation of salts, which leads to ionic toxicity, resulting in a nutritional imbalance and decreased transport. This, in turn, alters the metabolic processes, primarily at the level of photosynthesis (Ismail & Horie, 2017; Munns & Tester, 2008).

Salinity affects leaf area expansion, photosynthetic machinery, and related traits through stomatal closure, decreased chlorophyll content, and altered chloroplast structure. This, in turn, affects the light reactions, primarily the quantum efficiency of photosystem II and CO_2 assimilation (Castillejo-Morales *et al*., 2021; Khalil *et al*., 2022; Pan *et al*., 2021). Salinity is reported to induce the denaturation of membrane proteins involved in photosynthesis (Bahmani *et al*., 2015) and the degradation of chlorophyll molecules through the elevation of enzyme activity related to chlorophyll degradation.

Salt stress disrupts key physiological processes in plants, impairing enzyme activity, increasing photorespiration, and triggering the accumulation of reactive oxygen species (ROS), which leads to oxidative stress (Fu & Yang, 2023).

This oxidative damage manifests as lipid peroxidation, membrane instability, and protein degradation (Bose *et al.*, 2014; Habib *et al.*, 2016). Additionally, salt stress weakens cellular integrity by reducing antioxidant defenses and disrupting osmotic balance (Bose *et al.*, 2014; Fu & Yang, 2023). It also interferes with nitrogen metabolism by inhibiting essential enzymes (Ashraf *et al.*, 2018). It hampers growth by reducing seed germination, root development, and biomass accumulation (Zhang *et al.*, 2019). Furthermore, salt stress alters hormonal balance, decreasing the levels of auxins, cytokinins, and gibberellins while increasing the levels of abscisic acid (ABA) (Zulfiqar & Ashraf, 2021). Collectively, these effects significantly reduce crop productivity (Ansari *et al.*, 2022).

Plant salt-response mechanisms

The most important mechanisms that plants have for enhancing their tolerance to salt stress are enzymatic and non-enzymatic detoxification mechanisms, which efficiently sweep up reactive oxygen species (ROS) and involve changes in the cell wall (Mbarki *et al.*, 2018). Enzymatic mechanisms include superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione reductase (GR) (Fu & Yang, 2023; Laus *et al.*, 2021). The primary non-enzymatic water-soluble antioxidants include ascorbate (AsA), reduced glutathione (GSH), and phenols, as well as lipid-soluble compounds such as tocopherols and carotenoids (Apel & Hirt, 2004; Hasanuzzaman *et al.*, 2021). An increase in the antioxidant activity of the plants under salinity could be a good indicator of salt tolerance (Abbas *et al.*, 2022; Nigam *et al.*, 2022).

Another mechanism to cope with salinity stress is osmotic regulation. Ibrahimova *et al.* (2021) mention that several compounds called osmoprotectants are involved in the osmotic regulation of plants, such as sucrose, sorbitol, mannitol, glycerol, arabinitol, pinitol (carbohydrates), proteins, glutamate, aspartate, glycine, proline (nitrogen compounds), malate, and oxalate (organic compounds) (Gupta & Huang, 2014). These compounds maintain a lower water potential within the cells, preventing dehydration and protecting cell structure and biomolecules. Nigam *et al.* (2022) reported that the induction of osmoprotectants is strongly related to improved salt tolerance.

The synthesis and accumulation of stress proteins are another important mechanism for salt tolerance. Some of these proteins include Ca-binding proteins of the plasma membrane involved in signal transduction, such as annexin (Parihar *et al.*, 2015), cytochrome b6-f, ATP synthase subunit c, germin-like proteins, S-adenosylmethionine synthase protein (Kamal *et al.*, 2012), and aquaporins. Other essential proteins include the Heat Shock Proteins (HSP) family, acting as a chaperon; jacalin lectin, which is involved in protein-saccharide interactions and signal transduction; and osmotic, one of the proteins associated with osmotic stress (Ibrahimova *et al.*, 2021).

At the molecular level, plants can respond to or tolerate salt stress by activating enzymes and transcription factors. Kinases and phosphatases play a crucial role in stress signal transduction, modifying proteins to trigger adaptive responses. Among the most critical regulators are Heat Shock Factors (HSFs), which activate heat shock proteins (HSPs) that protect cellular structures, stabilize enzymes, and prevent protein denaturation in response to stress. Additionally, CBF/DREB (C-repeat-binding factor/Dehydration-Responsive Element-Binding Protein). This family of transcription factors binds to drought- and cold-responsive elements in DNA, enhancing the expression of genes that improve osmotic adjustment and antioxidant defense; ABF/ABRE (ABA-Responsive Element Binding Factor/ABA-Responsive Element, when abscisic acid, (ABA) levels rise under stress, these factors bind to ABA-responsive promoter elements, activating genes involved in stomatal closure, ion homeostasis, and stress tolerance (Bahmani *et al.*, 2015; Zhang *et al.*, 2013). The response also includes osmo-sensors (such as ATHK1), phospholipid-cleaving enzymes, and the critical secondary messengers such as Ca^{2+}, PtdOH, ROS, metabolic phosphatases, Ca-dependent protein kinases, serine/threonine protein kinase, mitogen-activated protein kinase cascades, two-component histidine kinases, and Ca/calmodulin-activated serine/threonine-specific protein phosphatases (Bahmani *et al.*, 2015). As salinity tolerance is controlled by the interaction of several genes, it encompasses numerous physiological and biochemical processes that interact with one another to resist salt stress at the molecular, cellular, and whole plant levels (Acharya *et al.*, 2022; Bahmani *et al.*, 2015; Ismail *et al.*, 2007). The authors include an extracellular salt sensor, monocation-induced $[Ca^{2+}]$. It increases 1 (MOCA1), as well as Glycosyl inositol phosphorylceramide (GIPC), the salt overly sensitive (SOS) pathway (Acharya *et al.*, 2022; Chen *et al.*, 2025; Zhu, 2001).

NaCl is the most common salt causing soil salinity. In this regard, essential mechanisms that have been reported include membrane Na^+ transport systems functioning in avoidance of Na^+ toxicity, Na^+ efflux from roots to the rhizosphere, Na^+ sequestration in vacuoles, loading and unloading at the xylem, ROS signaling, essential Na^+ transport systems for plant salt tolerance, channels for Na^+ influx into roots, channels and transporters that affect K^+ homeostasis and Cl^- transport and homeostasis (Ismail & Horie, 2017). It is possible to increase gene expression of *NHX1* (Na^+/H^+ antiporter), which regulates Na^+ sequestration in vacuoles to maintain osmotic balance (Chen *et al*., 2025; Zhu, 2001).

Van Zelm *et al.* (2020) report that ABA is the primary plant regulator responsible for signaling salt and osmotic stress in guard cells and root tissues, regulating the process of growth and development. The same authors indicated that, by targeting and phosphorylating downstream components, both ABA-independent sucrose non-fermenting 1–related protein kinase 2 (SnRK 2) and ABA-dependent SnRKs have essential roles in transcriptional regulation and post-transcriptional regulation during a salt stress response. A graphical summary of saline stress in plant physiology is shown in Figure 1.

Salt stress mitigation alternatives

Several strategies have been evaluated to mitigate salt stress, some of which are summarized in Table 1. Various types of nanoparticles and nanofertilizers have shown promising results so far in managing salt stress; for more details, we recommend consulting the review by Zulfiqar and Ashraf (2021). Regarding mineral nutrition, the use of silicon has garnered attention as a beneficial element that confers tolerance to different types of stress, including salinity stress, mainly by increasing antioxidant capacity (El-Serafy *et al*., 2021). The beneficial effect of potassium under salinity stress is also promising, primarily because its ion plays a crucial role in various processes, including enzymatic

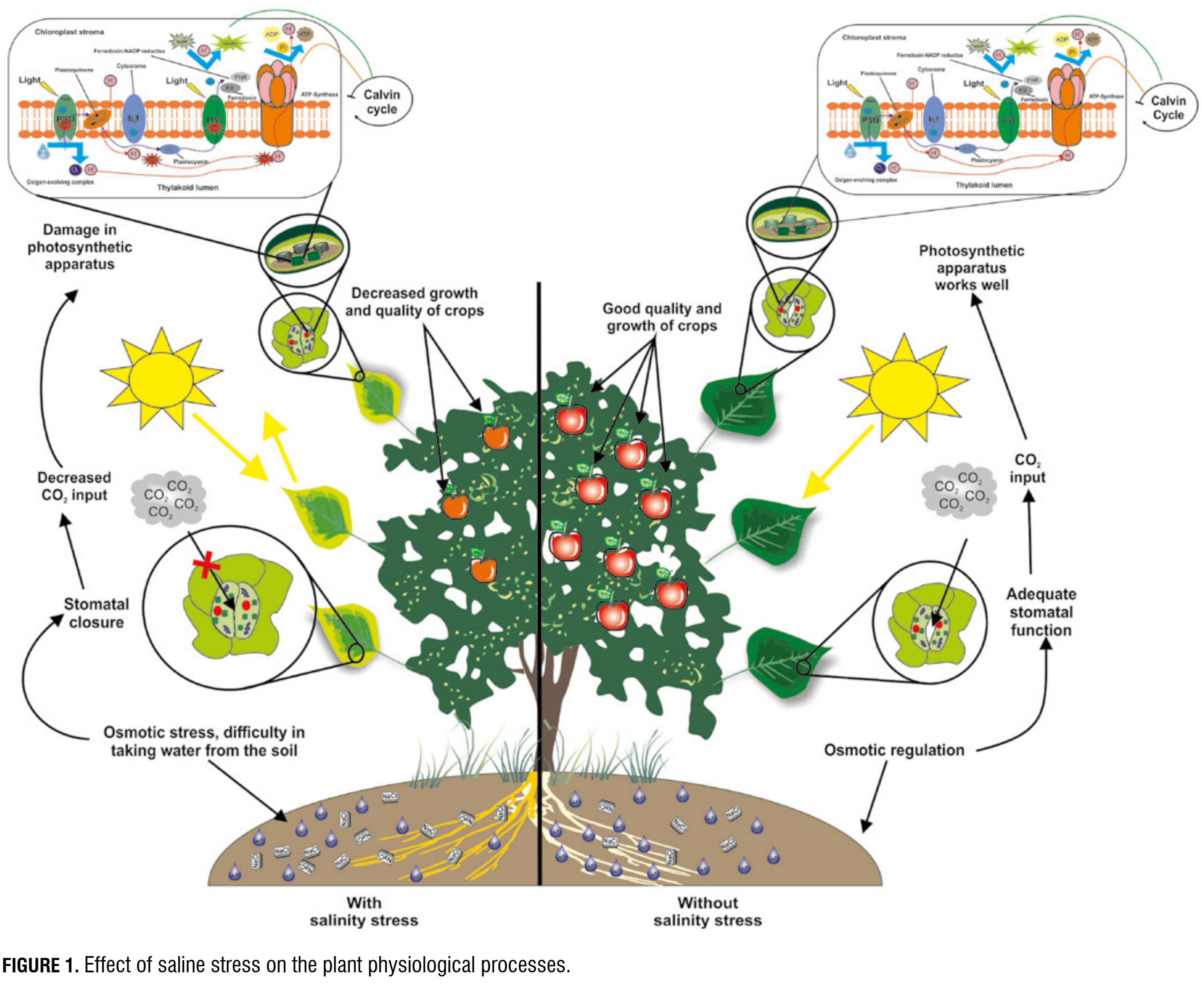

FIGURE 1. Effect of saline stress on the plant physiological processes.

activation, protein synthesis, photosynthesis, stomatal regulation, cation-anion balance, energy transmission, and osmoregulation (Abbas *et al*., 2022).

Some studies have indicated that salt tolerance can be conferred to various plant species with exogenous applications of signaling molecules such as nitric oxide and hydrogen peroxide, protectants such as glycine-betaine and proline, and trace elements such as zinc and cobalt (Altaf *et al*., 2020; Brengi *et al*., 2022; Negrão *et al*., 2017; Parihar *et al*., 2015). Others have reported this effect through plant regulators, mainly abscisic acid, jasmonic acid, brassinosteroids, salicylic acid, and melatonin (Assaf *et al*., 2022; Brengi *et al*., 2022). Through genetic improvement, it is also possible to efficiently reduce the effects of salinity. For example, in potato plants, the overexpression of the *StCYS1* gene results in the accumulation of more proline and chlorophyll, thereby enhancing the plant's resistance to high salinity. The transgenic approach facilitates the overexpression of several vital genes, including *DREB, MYB, COMT, SOS, PKE,* and *NHX*, which confers salt stress tolerance (Ibrahimova *et al*., 2021; Zhang *et al*., 2013). In alfalfa, overexpression of an ABA-inducible homeodomain-leucine zipper I gene *MsHB7* confers salt stress (Li *et al*., 2022).

Managing sustainable crop production under soil salinity conditions will be a significant challenge in the coming years (Nigam *et al*., 2022). The use of microorganisms is a more sustainable alternative to address this challenge. Recently, the role of PGPB in inducing salt stress tolerance through various mechanisms has been reported, with auspicious results for agricultural production (Ali *et al*., 2022; Kushwaha *et al*., 2020; Nigam *et al*., 2022; Sun *et al*., 2025). In this regard, Bullaín *et al*. (2022) report that the ECM fungus *Scleroderma bermudense* improved salt tolerance in seagrape seedlings. The inhibitory effect of NaCl stress on maize seed germination and seedling growth was mitigated by *Bacillus subtilis* HS5B5 (Bullaín Galardis *et al*., 2022). Sun *et al*. (2025) found that *Glutamicibacter endophyticus* J2-5-19 resists salt stress by expelling sodium ions and taking up potassium ions through Na^+/H^+ antiporters, and K^+ uptake proteins while also accumulating compatible solutes such as betaine, proline, and trehalose. Therefore, it has the potential for the development of microbial inoculants.

Plant growth-promoting bacteria

Plant growth-promoting bacteria (PGPB) are defined as free-living or endophytic bacteria that can directly or indirectly affect optimal biotic conditions for plants or mitigate

TABLE 1. Some mitigation strategies for salt stress in plants.

Salt stress mitigation alternative	Crop	Response	References
Nanoparticles	Pea (*Pisum saivum* L.)	Stimulated cyclic electron transport around photosystem I, thus protecting its photochemical activity.	(Mohamed *et al*., 2017)
Silicon	Sweet pea (*Lathyrus odoratus*)	Improved photosynthetic pigments, antioxidant activity, and phenolic compounds.	(El-Serafy *et al*., 2021)
Potassium	Wheat (*Triticum aestivum*)	Improved stomatal conductance, photosynthetic pigments, and antioxidant enzymes.	(Abbas *et al*., 2022)
Melatonin	Tomato (*Solanum lycopersicum*)	Improved redox homeostasis by the antioxidant system.	(Altaf *et al*., 2020)
Melatonin and Cobalt	Cucumber (*Cucumis sativus* L.)	Both treatments increased protein content, essential nutrient content, and catalase (CAT) activity.	(Brengi *et al*., 2022)
Salicylic acid	Barley (*Hordeum vulgare*)	Increased the content of calcium, iron, magnesium, and potassium while lowering the concentrations of sodium and malondialdehyde and electrolyte leakage.	(El-Esawi *et al*., 2017)
Abscisic acid	Tomato (*Solanum lycopersicum*)	Increased antioxidant capacity, proline content, and decreased stomatal conductance, ROS, and MDA.	(Hu *et al*., 2021)
Overexpression of *StCYS1* gene	Potato (*Solanum tuberosum* L.) plant	Transgenic plants accumulated more proline and chlorophyll, significantly increasing their resistance to high salinity.	(Liu *et al*., 2020)
Humic acid	Sorghum (*Sorghum bicolor* L.)	Improved water relations, stomatal conductance, and activation of the antioxidant enzymes (CAT, POD, and SOD).	(Ali *et al*., 2019; Hatami *et al*., 2018)
Mycorrhizal	Seagrape (*Coccoloba uvifera* L.)	Beneficial effects on the photosynthetic and transpiration rates, chlorophyll fluorescence and content, stomatal conductance, and water status.	(Bullaín Galardis *et al*., 2022)
Salicylic acid and PGPB (*Stenotrophomonas* sp.)	Spinach (*Spinacia oleracea* L.) and soybean (*Glycine max*)	Improve plant growth and yield, enhanced relative water contents, accumulated osmolytes, and increased enzymatic and non-enzymatic antioxidants.	(Nigam *et al*., 2022)

the effects of abiotic stress. These bacteria establish various relationships with plants that can be beneficial or harmful. These relationships can be symbiotic or non-symbiotic and are useful when regulatory substances are produced that enhance the plant's growth but detrimental when they are pathogenic (Di Benedetto *et al*., 2017). There are various mechanisms by which these relationships can directly affect the metabolism of plants, providing them substances necessary for their growth. These include the following: (1) nitrogen fixation, these bacteria are called diazotrophic bacteria and can fix atmospheric nitrogen and convert it to ammonium using a nitrogenase enzyme, a mechanism known as biological nitrogen fixation (BNF) (Pankievicz *et al*., 2021); (2) phosphate solubilization, bacteria solubilize phosphorus through the production of organic acid that reduce soil pH, converting them to more soluble forms that can be absorbed by plants, with the most common soluble form of P capable of absorption by plants being $H_2PO_4^-$ (Billah *et al*., 2019); and (3) production of plant hormones (Bashan & de Bashan, 2005), bacteria produce molecules that can affect plant development such auxins (indole-3-acetic acid (IAA)), abscisic acid (ABA) (Çakmakçı *et al*., 2020), gibberellins (Nett *et al*., 2017), and cytokinins. On the other hand, some mechanisms indirectly prevent the effects of phytopathogenic microorganisms by producing substances that inhibit microbial growth, alter the plant's metabolism, and increase resistance to infection (Bashan & de Bashan, 2005).

PGPBs have been studied for their mechanisms of action and potential applications. Most studies have focused on their ability to enhance the growth and productivity of commercial crops (Souza *et al*., 2015). Additionally, PGPBs have been explored for their role in ecological restoration, particularly in reforestation and rehabilitation of degraded soils (Bashan *et al*., 2012; Lopez *et al*., 2012). Beyond agriculture, PGPBs have been utilized in environmental biotechnology, such as wastewater treatment, when combined with microalgae (Choix *et al*., 2014; Glick, 2012; Palacios *et al*., 2014). They are also key components in the development of biofertilizers and bioinoculants, offering sustainable alternatives to chemical inputs.

Many bacteria have been identified and used commercially as plant growth promoters, including the genera *Bacillus, Agrobacterium, Azotobacter, Azospirillum, Serratia, Streptomyces,* and *Pseudomonas,* among others.

At the molecular level, various studies have been conducted to identify the genes that are involved in the mechanisms of action of PGPB and their interaction with plants. Jijón-Moreno *et al*. (2015) investigated the *ipdC*, *hisC1*, and *hisC2* genes, which are involved in the production of indole acetic acid in *Azospirillum brasilense*. Wisniewski-Dye *et al*. (2012) sequenced the complete genome of the *A. brasilense* CBG497. Romero *et al*. (2014) performed pyro sequencing of the 16S rRNA gene to identify the composition of endophytic bacteria present in tomato leaves. Finally, Bruto *et al*. (2014) studied 23 genes that provide 8 essential benefits for plants, finding that they can be associated and selected depending on the plant's habitat. They suggest that the PGPR condition is likely due to the accumulation of genes that contribute to the beneficial functions of plants associated with the bacteria associated with the roots.

One of the bacteria that has been most extensively studied for its ability to promote plant growth is *A. brasilense*. This was rediscovered by Döbereiner *et al*. in the 1970s and has since become a model bacterium for studying plant-growth bacteria (PGPBs). We recommend the article written by Cassán *et al*. (2020), which discusses the scientific impact and agricultural applications of this bacterium, as complementary literature on the use of *A. brasilense* as a model.

PGBP alleviates salt stress

To improve plant growth under saline stress conditions and achieve sustainable crop production, it is necessary to enhance salt stress tolerance in crops. Rhizobacteria can improve plant growth and crop productivity of the plants they colonize. *Bacillus* strains induce plant resistance to salt stress and produce various plant hormones that enhance growth (Rajendran *et al*., 2008).

PGPR, with the capacity to tolerate salinity conditions, can improve various processes in plants, enhancing germination, seedling vigor, root and shoot growth, and chlorophyll content, among other aspects (Bal *et al*., 2013; Sarkar *et al*., 2018). Ge and Zhang (2019) and Nigam *et al*. (2022) reported increased growth under salt stress after applying PGPB *Rhodopseudomonas palustris* and *Stenotrophomonas* sp., respectively. Increases in biomass due to PGPB can be attributed to the production and regulation of various plant regulators, such as auxins, which control gene expression by activating a family of transcription factors that perform distinct regulatory functions in plant cells (Numan *et al*., 2018).

PGPB (*Stenotrophomonas* sp.) evaluated in spinach and soybean plants induced K^+ and Ca^{++} uptake and reduced Na^+ uptake, even at a higher level compared to when salicylic acid was implicated. However, a higher Na^+/K^+ ratio under salt stress suggests that this defense mechanism is not highly influenced by the exogenous application of protectants (Nigam *et al*., 2022).

Some authors have suggested that PGPB is an effective regulator of photosynthesis due to its favorable influence on leaf structure, chloroplasts, and photosynthetic pigments (Barickman *et al*., 2014; Khan & Singh, 2008; Nigam *et al*., 2022; Salazar-Garcia *et al*., 2022). PGPB inoculation appears to enhance photosynthetic pigment synthesis by increasing the uptake of nitrogen, potassium, and phosphorus (Nigam *et al*., 2022).

Some PGPR produce antioxidant enzymes such as superoxide dismutase (SOD), peroxidase (POD), or catalase (CAT), which detoxify reactive oxygen species (ROS) in plants during salt stress (Han & Lee, 2005; Shultana *et al*., 2021). Increased antioxidant enzyme activities and upregulation of ROS pathway genes (CAT, APX, GR, and DHAR) were observed in PGPR-inoculated okra plants under salinity stress (Habib *et al*., 2016). However, PGPR can also produce compatible solutes such as proline, an abundant osmolyte in plants, which accumulates in response to osmotic stress induced by factors like drought and salinity (Fazal & Bano, 2016; Galinski & Trüper, 1994; Landa-faz *et al*., 2021; Sun *et al*., 2025). For this reason, PGPR can induce changes in total protein, IAA concentration, total sugar, and ethylene in plants, a process that may enhance tolerance to abiotic stress (Sarkar *et al*., 2018; Upadhyay *et al*., 2011; Yang *et al*., 2009) through induced systemic tolerance (Yang *et al*., 2009). On the other hand, *Enterobacter* sp. P23 was shown to promote rice seedling growth under salt stress by decreasing reactive oxygen species (ROS) and stress-induced ethylene; the latter process has been linked to 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity (Sarkar *et al*., 2018). ACC deaminase-containing PGPR can enhance the stress tolerance of plants by synthesizing plant hormones, facilitating mineral solubilization, increasing nutrient uptake, increasing leaf area, and improving chlorophyll and soluble protein content, as well as antioxidant enzyme activities (Dobbelaere *et al*., 2003). Saravanakumar and Samiyappan (2007) found that the ACC deaminase-containing *P. fluorescens* strain TDK1 increased the vigor index of groundnut seedlings using 120 mM of salt stress.

Bacterial exopolysaccharide (EPS) can also help mitigate salinity stress by reducing the content of Na^+ available for plant uptake (Upadhyay *et al*., 2011). Bacterial polysaccharides are macromolecules that include peptidoglycan, lipopolysaccharides, and exopolysaccharides. These acid water-soluble acids play a role in host-pathogen interactions and serve as structural components of the cell wall, such as peptidoglycan. These compounds function as biologically active substances, promoting bacterial and plant growth while facilitating surface adhesion and preventing desiccation (Shultana *et al*., 2022).

Inoculants

The term "inoculant" can refer to a bioformulation or biofertilizer and is defined as a matrix that contains one or more microorganisms, is easy to use, can improve the growth of plants (Arora *et al*., 2010), and acts as a system to control pests and diseases (Preininger *et al*., 2018). The oldest microorganism used as an inoculant is rhizobia, which can colonize the roots of plants and form nodules (Santos *et al*., 2019). The commercialization of inoculants began at the end of the seventies in India, where it is produced at a large scale today (Yadav & Chandra, 2014). The first patent of inoculant was registered in the USA in 1896 (Santos *et al*., 2019). The use of bacterial inoculants has been widely studied and is gaining strength over time in many developed countries (Glick, 2012).

The use of PGPBs in agriculture and soil restoration suggests that alternatives should be sought that allow the inoculation of the bacteria in plants and, above all, guarantee the effectiveness of the inoculum at the time of application, limit the effect of endogenous bacteria that can compete with the inoculant and determine the consortia that can be used (Bashan *et al*., 2002). On the other hand, the physical characteristics of the inoculant must be considered, such as whether it is liquid or dry and whether the organisms used are latent or not, as well as the timing of when the bacteria are released from the inoculant. In this regard, several methods are available for performing the inoculation. In direct methods, bacteria are incorporated directly into the plants, either physically or through application to the root or the leaves. Meanwhile, indirect methods involve a matrix in which the bacteria are embedded in various inner matrices, allowing them to be released gradually over time. This serves as a protection system against endogenous bacteria, allowing the number of bacteria added to the plant or the ground to be controlled. We suggest reading the review by Bashan *et al*. (2014), which discusses technological perspectives and inoculant formulations. Here, we present various methods for applying inoculants (Fig. 2).

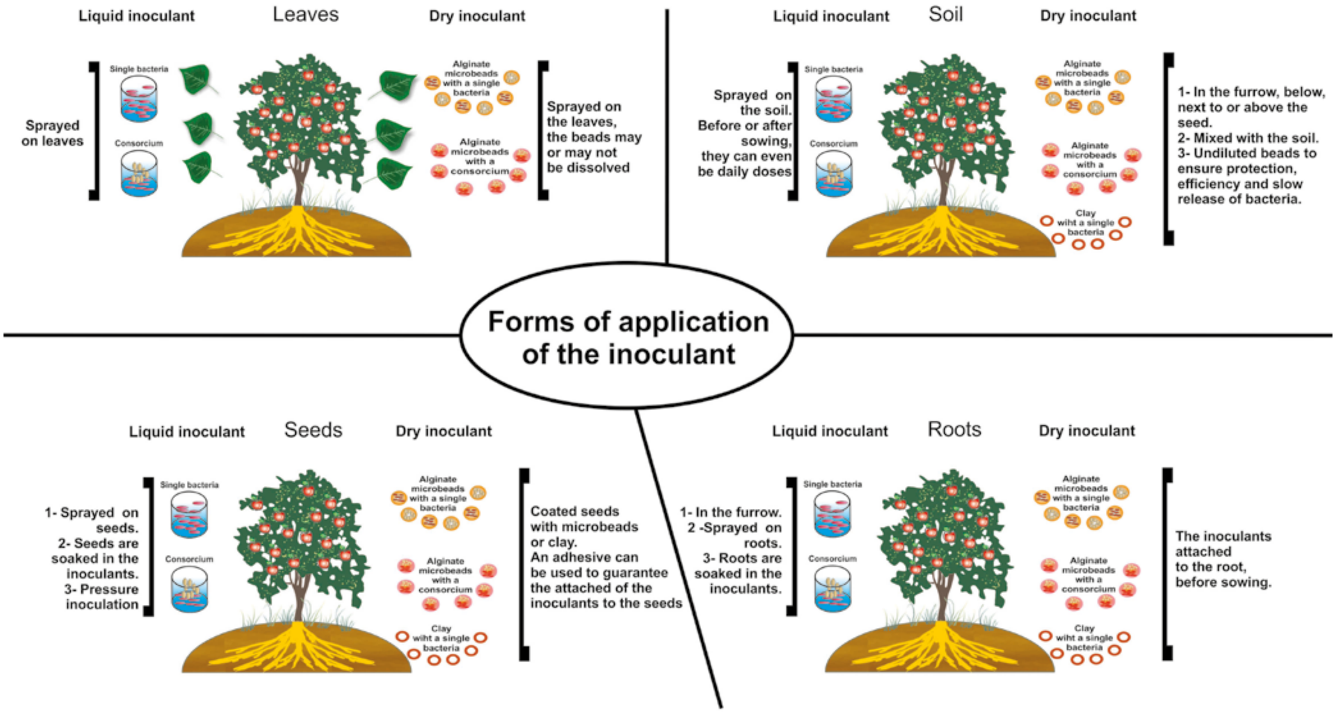

FIGURE 2. Forms of applications of the inoculant in plants.

Recent studies into PGPB have made significant progress, opening new opportunities for the formulation and creation of new inoculants or biofertilizers. These can be used not only for agricultural production but also to mitigate the effects of climate change through forest recovery of different ecosystems (Jack *et al*., 2021). However, despite the advances made in PGPB, the application of these microorganisms for crop improvement continues to be delayed and not widely explored (Baez-Rogelio *et al*., 2017).

To produce inoculants, several factors must be considered. First, the effectiveness of the bacteria and the type of technology to be used in making the inoculant must be known. Secondly, the type of application that will be made to the crop must be identified. Inoculants can be liquid or dry. Liquid inoculants are efficient in some respects; however, their shelf life is very short, and it is generally challenging to control the population of microorganisms. These inoculants are used in the rhizosphere, where they are added to the soil, allowing the roots to interact with the inoculant and then sowing the plant. Alternatively, the seed can even be inoculated by including it in the inoculant, through pressure changes to ensure that the bacteria enter the seed or by spraying in the foliar zone (Bashan *et al*., 2014; Preininger *et al*., 2018). Dry inoculants are typically produced within an inert matrix, which provides them some advantages over liquid inoculants. In general, matrices are used that provide the controlled release of microorganisms, guaranteeing their viability (Albareda *et al*., 2008; Covarrubias *et al*., 2012) and enabling the inclusion of one or more organisms without producing secondary effects on plants or the environment. Several commercial products available on the market vary in shape, composition, and application methods. They can be found in powder, liquid, and granular form. Most commercial inoculant products are peat-based because of their ease of use and their success in supporting rhizobium growth (Buntić *et al*., 2019). Several studies have been conducted to compare the efficiency of liquid inoculants and solid inoculants. Some of the results are presented in Table 2.

TABLE 2. Different types of inoculants and microorganism tests.

Type of Inoculant	Microorganisms	Crops	Effects	References
Encapsulation in alginate, skimmed milk for release	*Azospirillum brasilense*	Wheat and tomato plants	The dry weight of leaves and roots of wheat and tomato seedlings after 21 d was higher for those grown with the inoculant than without	(Bashan *et al*., 2002)
Liquid and peats	*Sinorhizobium* (Ensifer) *fredii* SMH12 or *Bradyrhizobium japonicum* USDA110	Soybean	Both types of inoculants used presented a similar seed yield	(Albareda *et al*., 2008)
Liquid and zeolite	*Bacillus subtilis, B. megaterium, A. chroococcum,* and *A. vinelandii*		All bacteria growth after 28 d of preparation of the inoculants	(Hindersah *et al*., 2021)
Liquid supplemented with agar, alginate, calcium chloride, glycerol, and ferric chloride	*Sinorhizobium meliloti* L3Si	Alfalfa seed	Bacteria can grow in liquid with supplements. Alfalfa can grow with the inoculant	(Buntic *et al*., 2019)
Liquid with exopolysaccharides	*Bradyrhizobium elkanii,* B. *japonicum*, *Bradyrhizobium viridifuturi symbiovar tropici*	Cowpea and soybean	Exopolysaccharides increase the viability of *Bradyrhizobium*, enhancing both plant growth and the viability of all inoculants	(Farias *et al*., 2022)
Liquid	*Enterobacter cloacae*	*Zea mays*	Enhancing maize growth and biomass	(Ali *et al*., 2022)

Conclusions

Saline stress is one of the significant challenges in agricultural production. This is due to the intensive use of chemical fertilizers, the overexploitation of soils, monoculture practices, and the water contamination by urban settlements, which continue to grow. Saline stress affects physiological processes in plants, including the photosynthetic machinery, and decreases the closing capacity of stomata, as well as the assimilation of CO_2.

However, plants have enzymatic and non-enzymatic mechanisms to control the effects of salinity. One of these is osmoregulation or the accumulation of proteins. However, the plant efforts to mitigate the impact of salt are very low due to its excess in the soil, so they are unable to balance the input of salt. In this regard, an alternative that has gained importance is the use of PGPBs. These halotolerant microorganisms can promote, stimulate, and protect plant growth. The use of these microorganisms as a fertilization system will allow crops to increase their production and reduce the use of chemical fertilizers, which contaminate soils and bodies of water. They will also be efficient tools for the conservation and restoration of forest areas, contributing to the preservation of biodiversity and adaptation to climate change.

PGPB has emerged as a valuable tool for the mitigation of salt stress in plants, particularly in crop production systems. Several studies have demonstrated the beneficial effects of PGPB in enhancing plant growth and tolerance to salinity stress. On the other hand, PGPB can enhance plant growth and development, even under saline conditions. They promote root and shoot growth, increase chlorophyll content, and enhance nutrient uptake, leading to improved crop productivity. PGPB can enhance the salt tolerance of crops through various mechanisms, producing and releasing plant hormones (such as auxins, cytokinins, and gibberellins) that stimulate plant growth and aid in mitigating salt stress mitigation. PGPB also produces organic acids and enzymes that improve nutrient availability and ion uptake, thereby reducing the toxic effects of salt.

Salt stress disrupts osmotic balance and ion homeostasis in plants. However, the use of PGPB can help in osmotic adjustment by synthesizing osmoprotectants (*e.g.*, proline) that maintain cellular water potential. They also facilitate the uptake of essentialions (*e.g.*, potassium) while excluding or reducing the uptake of toxic ions (*e.g.*, sodium), thus maintaining ion balance within the plant.

PGPB induces systemic resistance in plants, making them more resistant to salt stress and other biotic stresses. They activate the production of defense-related compounds, such as phytohormones, enzymes, and secondary metabolites, which help plants defend against pathogens and other stressors.

PGPB forms biofilms on the root surface and establishes a strong rhizosphere competence. This enables them to colonize the plant roots effectively, compete with pathogens, and provide a continuous supply of growth-promoting substances to the plants.

The effectiveness of PGPB in mitigating salt stress may vary among different crop species. Some crops exhibit a higher degree of response to PGPB inoculation, while others may show more modest effects. It is crucial to select PGPB strains that are well-adapted to the target crop and its specific environmental conditions.

The use of PGPB as a tool to mitigate salt stress aligns with sustainable agricultural practices. PGPB can reduce the need for chemical fertilizers and pesticides, thereby minimizing environmental pollution. They also contribute to the overall health and biodiversity of the soil ecosystem.

Given the above, PGPB offers excellent potential as a tool to mitigate salt stress in crops. Their ability to enhance plant growth, improve salt tolerance, and induce systemic resistance makes them valuable allies in sustainable crop production systems, especially in saline environments. Further research is needed to explore the specific mechanisms of PGPB action and optimize their application for different crops and agroecosystems.

The review highlights the potential of plant growth-promoting bacteria as a biotechnological tool to mitigate salt stress in crops. However, it is necessary to strengthen research in aspects such as the selection of specific strains, compatibility with different agricultural systems, and the assessment of their long-term impact. This will enable their practical implementation in crop improvement programs and environmental sustainability initiatives.

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Conflict of interest statement

The authors declare that there is no conflict of interests regarding the publication of this article.

Author's contributions

Conceptualization: JPH, EAPO, and HEBL; writing—original draft preparation: JPH, EAPO, and HEBL; writing—review and editing: JPH, EAPO, and HEBL. This research received no external funding. All authors have read and approved the final version of the manuscript.

Literature cited

Abbas, G., Rehman, S., Siddiqui, M. H., Ali, H. M., Farooq, M. A., & Chen, Y. (2022). Potassium and humic acid synergistically increase salt tolerance and nutrient uptake in contrasting wheat genotypes through ionic homeostasis and activation of antioxidant enzymes. *Plants, 11*(3), Article 263. https://doi.org/10.3390/plants11030263

Acharya, B. R., Sandhu, D., Dueñas, C., Ferreira, J. F. S., & Grover, K. K. (2022). Deciphering molecular mechanisms involved in salinity tolerance in guar (*Cyamopsis tetragonoloba* L. Taub.) using transcriptome analyses. *Plants, 11*, Article 291. https://doi.org/10.3390/plants11030291

Acosta-Motos, J. R., Ortuño, M. F., Bernal-Vicente, A., Díaz-Vivancos, P., Sánchez-Blanco, M. J., & Hernández, J. A. (2017). Plant responses to salt stress: Adaptive mechanisms. *Agronomy, 7*(1), Article 18. https://doi.org/10.3390/agronomy7010018

Albareda, M., Rodríguez-Navarro, D. N., Camacho, M., & Temprano, F. J. (2008). Alternatives to peat as a carrier for rhizobia inoculants: Solid and liquid formulations. *Soil Biology and Biochemistry, 40*(11), 2771–2779. https://doi.org/10.1016/j.soilbio.2008.07.021

Ali, A. Y. A., Ibrahim, M. E. H., Zhou, G., Nimir, N. E. A., Jiao, X., Zhu, G., Elsiddig, A. M. I., Zhi, W., Chen, X., & Lu, H. (2019). Ameliorative effects of jasmonic acid and humic acid on antioxidant enzymes and salt tolerance of forage sorghum under salinity conditions. *Agronomy Journal, 111*(6), 3099–3108. https://doi.org/10.2134/agronj2019.05.0347

Ali, B., Wang, X., Saleem, M. H., Sumaira, A., Hafeez, A., Afridi, M. S., Khan, S., Zaib-Un-Nisa, Ullah, I., Amaral Júnior, A. T., Alatawi, A., & Ali, S. (2022). PGPR-mediated salt tolerance in maize by modulating plant physiology, antioxidant defense, compatible solutes accumulation and biosurfactant-producing genes. *Plants, 11*(3), Article 345. https://doi.org/10.3390/plants11030345

Altaf, M. A., Shahid, R., Ren, M. X., Naz, S., Altaf, M. M., Qadir, A., Anwar, M., Shakoor, A., & Hayat, F. (2020). Exogenous melatonin enhances salt stress tolerance in tomato seedlings. *Biologia Plantarum, 64*, 604–615. https://doi.org/10.32615/bp.2020.090

Ansari, H. H., Siddiqui, A., Wajid, D., Tabassum, S., Umar, M., & Siddiqui, Z. S. (2022). Profiling of energy compartmentalization in photosystem II (PSII), light harvesting complexes and specific energy fluxes of primed maize cultivar (P1429) under salt stress environment. *Plant Physiology and Biochemistry, 170*, 296–306. https://doi.org/10.1016/j.plaphy.2021.12.015

Apel, K., & Hirt, H. (2004). Reactive oxygen species: Metabolism, oxidative stress, and signal transduction. *Annual Review of Plant Biology, 55*(1), 373–399. https://doi.org/10.1146/annurev.arplant.55.031903.141701

Arora, N. K., Khare, E., & Maheshwari, D. K. (2010). Plant growth promoting rhizobacteria: Constraints in bioformulation, commercialization, and future strategies. In D. K. Maheshwari (Ed.), *Plant growth and health promoting bacteria* (pp. 97–116). Springer. https://doi.org/10.1007/978-3-642-13612-2_5

Ashraf, M., Shahzad, S. M., Imtiaz, M., & Rizwan, M. S. (2018). Salinity effects on nitrogen metabolism in plants – Focusing on the activities of nitrogen metabolizing enzymes: A review. *Journal of Plant Nutrition, 41*(8), 1065–1081. https://doi.org/10.1080/01904167.2018.1431670

Assaf, M., Korkmaz, A., Karaman, Ş., & Kulak, M. (2022). Effect of plant growth regulators and salt stress on secondary metabolite composition in Lamiaceae species. *South African Journal of Botany, 144*, 480–493. https://doi.org/10.1016/j.sajb.2021.10.030

Baez-Rogelio, A., Morales-García, Y. E., Quintero-Hernández, V., & Muñoz-Rojas, J. (2017). Next generation of microbial inoculants for agriculture and bioremediation. *Microbial Biotechnology, 10*(1), 19–21. https://doi.org/10.1111/1751-7915.12448

Bahmani, K., Noori, S. A. S., Darbandi, A. I., & Akbari, A. (2015). Molecular mechanisms of plant salinity tolerance: A review. *Australian Journal of Crop Science, 9*(4), 321–336. https://doi.org/10.3316/informit.132428657147758

Bal, H. B., Nayak, L., Das, S., & Adhya, T. K. (2013). Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. *Plant and Soil, 366*(1–2), 93–105. https://doi.org/10.1007/s11104-012-1402-5

Barickman, T. C., Kopsell, D. A., & Sams, C. E. (2014). Abscisic acid increases carotenoid and chlorophyll concentrations in leaves and fruit of two tomato genotypes. *Journal of the American Society for Horticultural Science, 139*(3), 261–266. https://doi.org/10.21273/JASHS.139.3.261

Bashan, Y., & de-Bashan, L. E. (2005). Bacteria/plant growth-promotion. In D. Hillel (Ed.), *Encyclopedia of soils in the environment* (pp. 103–115). Elsevier. https://www.researchgate.net/profile/Yoav-Bashan-2/publication/253953454_Bacteria_Plant_growth-promotion/links/0deec5345c04910e38000000/Bacteria-Plant-growth-promotion.pdf

Bashan, Y., de-Bashan, L. E., Prabhu, S. R., & Hernandez, J.-P. (2014). Advances in plant growth-promoting bacterial inoculant technology: Formulations and practical perspectives (1998–2013). *Plant and Soil, 378*(1–2), 1–33. https://doi.org/10.1007/s11104-013-1956-x

Bashan, Y., Hernandez, J.-P., Leyva, L. A., & Bacilio, M. (2002). Alginate microbeads as inoculant carriers for plant growth-promoting bacteria. *Biology and Fertility of Soils, 35*(5), 359–368. https://doi.org/10.1007/s00374-002-0481-5

Bashan, Y., & Holguín, G. (1998). Proposal for the division of plant growth-promoting rhizobacteria into two classifications: Biocontrol-PGPB (plant growth-promoting bacteria) and PGPB. *Soil Biology and Biochemistry, 30*(8–9), 1225–1228. https://doi.org/10.1016/S0038-0717(97)00187-9

Bashan, Y., Salazar, B. G., Moreno, M., López, B. R., & Linderman, R. G. (2012). Restoration of eroded soil in the Sonoran Desert with native leguminous trees using plant growth-promoting microorganisms and limited amounts of compost and water. *Journal of Environmental Management, 102*, 26–36. https://doi.org/10.1016/j.jenvman.2011.12.032

Bhise, K. K., & Dandge, P. B. (2019). Mitigation of salinity stress in plants using plant growth-promoting bacteria. *Symbiosis, 79*(3), 191–204. https://doi.org/10.1007/s13199-019-00638-y

Billah, M., Khan, M., Bano, A., Hassan, T. U., Munir, A., & Gurmani, A. R. (2019). Phosphorus and phosphate solubilizing bacteria: Keys for sustainable agriculture. *Geomicrobiology Journal, 36*(10), 904–916. https://doi.org/10.1080/01490451.2019.1654043

Bose, J., Rodrigo-Moreno, A., & Shabala, S. (2014). ROS homeostasis in halophytes in the context of salinity stress tolerance. *Journal of Experimental Botany, 65*(5), 1241–1257. https://doi.org/10.1093/jxb/ert430

Brengi, S. H., Khedr, A. A. E. M., & Abouelsaad, I. A. (2022). Effect of melatonin or cobalt on growth, yield and physiological responses of cucumber (*Cucumis sativus* L.) plants under salt stress. *Journal of the Saudi Society of Agricultural Sciences, 21*(1), 51–60. https://doi.org/10.1016/j.jssas.2021.06.012

Bruto, M., Prigent-Combaret, C., Müller, D., & Moënne-Loccoz, Y. (2014). Analysis of genes contributing to plant-beneficial functions in plant growth-promoting rhizobacteria and related Proteobacteria. *Scientific Reports, 4*(1), Article 6261. https://doi.org/10.1038/srep06261

Bullaín Galardis, M. M., López Sánchez, R. C., Fall, F., Eichler-Löbermann, B., Pruneau, L., & Bâ, A. M. (2022). Growth and physiological responses of ectomycorrhizal *Coccoloba uvifera* L. seedlings to salt stress. *Journal of Arid Environments, 196*, Article 104650. https://doi.org/10.1016/j.jaridenv.2021.104650

Buntic, A., Stajkovic-Srbinovic, O., Knezevic, M., Kuzmanovic, D., Rasulic, N., & Delic, D. (2019). Development of liquid rhizobial inoculants and pre-inoculation of alfalfa seeds. *Archives of Biological Sciences, 71*(2), 379–387. https://doi.org/10.2298/ABS181008062B

Çakmakçı, R., Mosber, G., Milton, A. H., Alatürk, F., & Ali, B. (2020). The effect of auxin and auxin-producing bacteria on the growth, essential oil yield, and composition in medicinal and aromatic plants. *Current Microbiology, 77*(4), 564–577. https://doi.org/10.1007/s00284-020-01917-4

Cassán, F., Coniglio, A., López, G., Molina, R., Nievas, S., de Carlan, C. L. N., Donadio, F., Torres, D., Rosas, S., Pedrosa, F. O., Souza, E., Zorita, M. D., de-Bashan, L. E., & Mora, V. (2020). Everything you must know about *Azospirillum* and its impact on agriculture and beyond. *Biology and Fertility of Soils, 56*(4), 461–479. https://doi.org/10.1007/s00374-020-01463-y

Castillejo-Morales, A., Jarma-Orozco, A., & Pompelli, M. F. (2021). Physiological and morphological features denote that salt stress in *Stevia rebaudiana* is based on nonstomatal instead of stomatal limitation. *Revista Colombiana de Ciencias Hortícolas, 15*(3), Article 12928. https://doi.org/10.17584/rcch.2021v15i3.12928

Chaves, M. M., Flexas, J., & Pinheiro, C. (2009). Photosynthesis under drought and salt stress: Regulation mechanisms from whole plant to cell. *Annals of Botany, 103*(4), 551–560. https://doi.org/10.1093/aob/mcn125

Chen, J., Bian, C., Fu, C., Zhang, Q., Qin, D., Hao, W., Guo, M., Huo, J., Li, J., & Gang, H. (2025). Overexpression of LcMYB90 transcription factor enhances drought and salt tolerance in blue honeysuckle (*Lonicera caerulea* L.) and tobacco (*Nicotiana tabacum* L.). *International Journal of Molecular Sciences, 26*(7), Article 3124. https://doi.org/10.3390/ijms26073124

Choix, F. J., Bashan, Y., Mendoza, A., & de-Bashan, L. E. (2014). Enhanced activity of ADP-glucose pyrophosphorylase and formation of starch induced by *Azospirillum brasilense* in *Chlorella vulgaris*. *Journal of Biotechnology, 177*, 22–34. https://doi.org/10.1016/j.jbiotec.2014.02.014

Covarrubias, S. A., de-Bashan, L. E., Moreno, M., & Bashan, Y. (2012). Alginate beads provide a beneficial physical barrier against native microorganisms in wastewater treated with immobilized bacteria and microalgae. *Applied Microbiology and Biotechnology, 93*(6), 2669–2680. https://doi.org/10.1007/s00253-011-3585-8

Di Benedetto, N. A., Corbo, M. R., Campaniello, D., Cataldi, M. P., Bevilacqua, A., Sinigaglia, M., & Flagella, Z. (2017). The role of plant growth-promoting bacteria in improving nitrogen use efficiency for sustainable crop production: A focus on wheat. *AIMS Microbiology, 3*(3), 413–434. https://doi.org/10.3934/microbiol.2017.3.413

Dobbelaere, S., Vanderleyden, J., & Okon, Y. (2003). Plant growth-promoting effects of diazotrophs in the rhizosphere. *Critical Reviews in Plant Sciences, 22*(2), 107–149. https://doi.org/10.1080/713610853

El-Esawi, M. A., Elansary, H. O., El-Shanhorey, N. A., Abdel-Hamid, A. M. E., Ali, H. M., & Elshikh, M. S. (2017). Salicylic acid-regulated antioxidant mechanisms and gene expression enhance rosemary performance under saline conditions. *Frontiers in Physiology, 8*, Article 716. https://doi.org/10.3389/fphys.2017.00716

El-Serafy, R. S., El-Sheshtawy, A.-N. A., Atteya, A. K. G., Al-Hashimi, A., Abbasi, A. M., & Al-Ashkar, I. (2021). Seed priming with silicon as a potential to increase salt stress tolerance in *Lathyrus odoratus*. *Plants, 10*(10), Article 2140. https://doi.org/10.3390/plants10102140

Farias, T. P., Soares, B. L., D'Eça, C. S. B., & Moreira, F. M. S. (2022). Polymeric formulations of liquid inoculants with rhizobia exopolysaccharides increase the survival and symbiotic efficiency of elite *Bradyrhizobium* strains. *Archives of Microbiology, 204*(3), Article 177. https://doi.org/10.1007/s00203-022-02779-z

Farouk, S., & Al-Amri, S. M. (2019). Exogenous melatonin-mediated modulation of arsenic tolerance with improved accretion of secondary metabolite production, activating antioxidant capacity and improved chloroplast ultrastructure in rosemary herb. *Ecotoxicology and Environmental Safety, 180*, 333–347. https://doi.org/10.1016/j.ecoenv.2019.05.021

Fasciglione, G., Casanovas, E. M., Quillehauquy, V., Yommi, A. K., Goñi, M. G., Roura, S. I., & Barassi, C. A. (2015). *Azospirillum* inoculation effects on growth, product quality and storage life of lettuce plants grown under salt stress. *Scientia Horticulturae, 195*, 154–162. https://doi.org/10.1016/j.scienta.2015.09.015

Fazal, A., & Bano, A. (2016). Role of plant growth-promoting rhizobacteria (PGPR), biochar, and chemical fertilizer under salinity stress. *Communications in Soil Science and Plant Analysis, 47*(17), 1985–1993. https://doi.org/10.1080/00103624.2016.1216562

Fu, H., & Yang, Y. (2023). How plants tolerate salt stress. *Current Issues in Molecular Biology, 45*(7), 5914–5934. https://doi.org/10.3390/cimb45070374

Galinski, E. A., & Trüper, H. G. (1994). Microbial behaviour in salt-stressed ecosystems. *FEMS Microbiology Reviews, 15*(2–3), 95–108. https://doi.org/10.1111/j.1574-6976.1994.tb00128.x

Ge, H., & Zhang, F. (2019). Growth-promoting ability of *Rhodopseudomonas palustris* G5 and its effect on induced resistance in cucumber against salt stress. *Journal of Plant Growth Regulation, 38*(1), 180–188. https://doi.org/10.1007/s00344-018-9825-8

Glick, B. R. (2012). Plant growth-promoting bacteria: Mechanisms and applications. *Scientifica, 2012*, 1–15. https://pmc.ncbi.nlm.nih.gov/articles/PMC3820493/

Gupta, B., & Huang, B. (2014). Mechanism of salinity tolerance in plants: Physiological, biochemical, and molecular characterization. *International Journal of Genomics, 2014*, 1–18. https://doi.org/10.1155/2014/701596

Habib, S. H., Kausar, H., & Saud, H. M. (2016). Plant growth-promoting rhizobacteria enhance salinity stress tolerance in okra through ROS-scavenging enzymes. *BioMed Research International, 2016*, 1–10. https://doi.org/10.1155/2016/6284547

Han, H. S., & Lee, K. D. (2005). Plant growth promoting rhizobacteria effect on antioxidant status, photosynthesis, mineral uptake and growth of lettuce under soil salinity. *Research Journal of Agriculture and Biological Sciences*, *1*(3), 210–215. https://www.aensiweb.net/AENSIWEB/rjabs/rjabs/210-215.pdf

Hasanuzzaman, M., Raihan, Md. R. H., Masud, A. A. C., Rahman, K., Nowroz, F., Rahman, M., Nahar, K., & Fujita, M. (2021). Regulation of reactive oxygen species and antioxidant defense in plants under salinity. *International Journal of Molecular Sciences*, *22*(17), Article 9326. https://doi.org/10.3390/ijms22179326

Hatami, E., Shokouhian, A. A., Ghanbari, A. R., & Naseri, L. A. (2018). Alleviating salt stress in almond rootstocks using humic acid. *Scientia Horticulturae, 237*, 296–302. https://doi.org/10.1016/j.scienta.2018.03.034

Hindersah, R., Rahmadina, I., Harryanto, R., Suryatmana, P., & Arifin, M. (2021). Bacillus and Azotobacter counts in solid biofertilizer with different concentration of zeolite and liquid inoculant. *IOP Conference Series: Earth and Environmental Science, 667*(1), Article 012010. https://doi.org/10.1088/1755-1315/667/1/012010

Hu, E., Liu, M., Zhou, R., Jiang, F., Sun, M., Wen, J., Zhu, Z., & Wu, Z. (2021). Relationship between melatonin and abscisic acid in response to salt stress of tomato. *Scientia Horticulturae, 285*, Article 110176. https://doi.org/10.1016/j.scienta.2021.110176

Ibrahimova, U., Kumari, P., Yadav, S., Rastogi, A., Antala, M., Suleymanova, Z., Zivcak, M., Tahjib-Ul-Arif, M., Hussain, S., Abdelhamid, M., Hajihashemi, S., Yang, X., & Brestic, M. (2021). Progress in understanding salt stress response in plants using biotechnological tools. *Journal of Biotechnology, 329*, 180–191. https://doi.org/10.1016/j.jbiotec.2021.02.007

Iglesias, A. A. (2020). *Genetic and physiological basis of cold tolerance in rice* [Doctoral dissertation, Universidad de Guadalajara].

Ismail, A. M., Heuer, S., Thomson, M. J., & Wissuwa, M. (2007). Genetic and genomic approaches to develop rice germplasm for problem soils. *Plant Molecular Biology, 65*(4), 547–570. https://doi.org/10.1007/s11103-007-9215-2

Ismail, A. M., & Horie, T. (2017). Genomics, physiology, and molecular breeding approaches for improving salt tolerance. *Annual Review of Plant Biology, 68*(1), 405–434. https://doi.org/10.1146/annurev-arplant-042916-040936

Jack, C. N., Petipas, R. H., Cheeke, T. E., Rowland, J. L., & Friesen, M. L. (2021). Microbial inoculants: Silver bullet or microbial Jurassic Park? *Trends in Microbiology, 29*(4), 299–308. https://doi.org/10.1016/j.tim.2020.11.006

Jijón-Moreno, S., Marcos-Jiménez, C., Pedraza, R. O., Ramírez-Mata, A., de Salamone, I. G., Fernández-Scavino, A., Vásquez-Hernández, C. A., Soto-Urzúa, L., & Baca, B. E. (2015). The *ipdC*, *hisC1* and *hisC2* genes involved in indole-3-acetic production used as alternative phylogenetic markers in *Azospirillum brasilense*. *Antonie van Leeuwenhoek, 107*(6), 1501–1517. https://doi.org/10.1007/s10482-015-0444-0

Kamal, A. H. M., Cho, K., Kim, D.-E., Uozumi, N., Chung, K.-Y., Lee, S. Y., Choi, J.-S., Cho, S.-W., Shin, C.-S., & Woo, S. H. (2012). Changes in physiology and protein abundance in salt-stressed wheat chloroplasts. *Molecular Biology Reports, 39*(9), 9059–9074. https://doi.org/10.1007/s11033-012-1777-7

Khalil, R., Yusuf, M., Bassuony, F., Haroun, S., & Gamal, A. (2022). Alpha-tocopherol reinforces selenium efficiency to ameliorate salt stress in maize plants through carbon metabolism, enhanced photosynthetic pigments and ion uptake. *South African Journal of Botany, 144*, 1–9. https://doi.org/10.1016/j.sajb.2021.08.033

Khan, P. S. S. V., & Basha, P. O. (2015). Salt stress and leguminous crops. In M. M. Azooz, & P. Ahmad (Eds.). *Legumes under environmental stress* (pp. 21–51). Wiley. https://doi.org/10.1002/9781118917091.ch2

Kushwaha, P., Kashyap, P. L., Bhardwaj, A. K., Kuppusamy, P., Srivastava, A. K., & Tiwari, R. K. (2020). Bacterial endophyte mediated plant tolerance to salinity: Growth responses and mechanisms of action. *World Journal of Microbiology and Biotechnology, 36*(2), Article 26. https://doi.org/10.1007/s11274-020-2804-9

Landa-Faz, A., González-Orenga, S., Boscaiu, M., Rodríguez-Vázquez, R., & Vicente, O. (2021). Effect of the pesticide endosulfan and two different biostimulants on the stress responses of *Phaseolus leptostachyus* plants grown in a saline soil. *Agronomy, 11*(6), Article 1208. https://doi.org/10.3390/agronomy11061208

Laus, M. N., De Santis, M. A., Flagella, Z., & Soccio, M. (2021). Changes in antioxidant defence system in durum wheat under hyperosmotic stress: A concise overview. *Plants, 11*(1), Article 98. https://doi.org/10.3390/plants11010098

Leyva, L. A., Bashan, Y., Mendoza, A., & de-Bashan, L. E. (2014). Accumulation of fatty acids in *Chlorella vulgaris* under heterotrophic conditions in relation to activity of acetyl-CoA carboxylase, temperature, and co-immobilization with *Azospirillum brasilense*. *Naturwissenschaften, 101*(10), 819–830. https://doi.org/10.1007/s00114-014-1223-x

Li, X., Hou, Y., Li, M., Zhang, F., Yi, F., Kang, J., Yang, Q., & Long, R. (2022). Overexpression of an ABA-inducible homeodomain-leucine zipper I gene *MsHB7* confers salt stress sensitivity to alfalfa. *Industrial Crops and Products, 177*, Article 114463. https://doi.org/10.1016/j.indcrop.2021.114463

Liu, M., Li, Y., Li, G., Dong, T., Liu, S., Liu, P., & Wang, Q. (2020). Overexpression of *StCYS1* gene enhances tolerance to salt stress in the transgenic potato (*Solanum tuberosum* L.) plant. *Journal of Integrative Agriculture, 19*(9), 2239–2246. https://doi.org/10.1016/S2095-3119(20)63262-2

López, B. R., Tinoco-Ojanguren, C., Bacilio, M., Mendoza, A., & Bashan, Y. (2012). Endophytic bacteria of the rock-dwelling cactus *Mammillaria fraileana* affect plant growth and mobilization of elements from rocks. *Environmental and Experimental Botany, 81*, 26–36. https://doi.org/10.1016/j.envexpbot.2012.02.014

López-Lozano, N. E., Carcaño-Montiel, M. G., & Bashan, Y. (2016). Using native trees and cacti to improve soil potential nitrogen fixation during long-term restoration of arid lands. *Plant and Soil, 403*(1–2), 317–329. https://doi.org/10.1007/s11104-016-2807-3

Mbarki, S., Sytar, O., Cerda, A., Zivcak, M., Rastogi, A., He, X., Zoghlami, A., Abdelly, C., & Brestic, M. (2018). Strategies to mitigate the salt stress effects on photosynthetic apparatus and productivity of crop plants. In V. Kumar, S. Wani, P. Suprasanna, & L. S. Tran (Eds.). *Salinity responses and tolerance in plants* (Vol. 1, pp. 85–136). Springer International Publishing. https://doi.org/10.1007/978-3-319-75671-4_4

Mohamed, A. K. S. H., Qayyum, M. F., Abdel-Hadi, A. M., Rehman, R. A., Ali, S., & Rizwan, M. (2017). Interactive effect of salinity and silver nanoparticles on photosynthetic and biochemical parameters of wheat. *Archives of Agronomy and Soil Science, 63*(12), 1736–1747. https://doi.org/10.1080/03650340.2017.1300256

Moreno, M., de-Bashan, L. E., Hernandez, J.-P., López, B. R., & Bashan, Y. (2017). Success of long-term restoration of degraded arid land using native trees planted 11 years earlier. *Plant and Soil, 421*(1–2), 83–92. https://doi.org/10.1007/s11104-017-3438-z

Munns, R., & Tester, M. (2008). Mechanisms of salinity tolerance. *Annual Review of Plant Biology, 59*(1), 651–681. https://doi.org/10.1146/annurev.arplant.59.032607.092911

Negrão, S., Schmöckel, S. M., & Tester, M. (2017). Evaluating physiological responses of plants to salinity stress. *Annals of Botany, 119*(1), 1–11. https://doi.org/10.1093/aob/mcw191

Nett, R. S., Montanares, M., Marcassa, A., Lu, X., Nagel, R., Charles, T. C., Hedden, P., Rojas, M. C., & Peters, R. J. (2017). Elucidation of gibberellin biosynthesis in bacteria reveals convergent evolution. *Nature Chemical Biology, 13*(1), 69–74. https://doi.org/10.1038/nchembio.2232

Nigam, B., Dubey, R. S., & Rathore, D. (2022). Protective role of exogenously supplied salicylic acid and PGPB (*Stenotrophomonas* sp.) on spinach and soybean cultivars grown under salt stress. *Scientia Horticulturae, 293*, Article 110654. https://doi.org/10.1016/j.scienta.2021.110654

Numan, M., Bashir, S., Khan, Y., Mumtaz, R., Shinwari, Z. K., Khan, A. L., Khan, A., & Al-Harrasi, A. (2018). Plant growth promoting bacteria as an alternative strategy for salt tolerance in plants: A review. *Microbiological Research, 209*, 21–32. https://doi.org/10.1016/j.micres.2018.02.003

Palacios, O. A., Bashan, Y., & de-Bashan, L. E. (2014). Proven and potential involvement of vitamins in interactions of plants with plant growth-promoting bacteria – An overview. *Biology and Fertility of Soils, 50*(3), 415–432. https://doi.org/10.1007/s00374-013-0894-3

Pan, T., Liu, M., Kreslavski, V. D., Zharmukhamedov, S. K., Nie, C., Yu, M., Kuznetsov, V. V., Allakhverdiev, S. I., & Shabala, S. (2021). Non-stomatal limitation of photosynthesis by soil salinity. *Critical Reviews in Environmental Science and Technology, 51*(8), 791–825. https://doi.org/10.1080/10643389.2020.1735231

Pankievicz, V. C. S., Amaral, F. P., Ané, J.-M., & Stacey, G. (2021). Diazotrophic bacteria and their mechanisms to interact and benefit cereals. *Molecular Plant-Microbe Interactions, 34*(5), 491–498. https://doi.org/10.1094/MPMI-11-20-0316-FI

Parihar, P., Singh, S., Singh, R., Singh, V. P., & Prasad, S. M. (2015). Effect of salinity stress on plants and its tolerance strategies: A review. *Environmental Science and Pollution Research, 22*(6), 4056–4075. https://doi.org/10.1007/s11356-014-3739-1

Pasternak, T., Groot, E. P., Kazantsev, F. V., Teale, W., Omelyanchuk, N., Kovrizhnykh, V., Palme, K., & Mironova, V. V. (2019). Salicylic acid affects root meristem patterning via auxin distribution in a concentration-dependent manner. *Plant Physiology, 180*(3), 1725–1739. https://doi.org/10.1104/pp.19.00130

Preininger, C., Sauer, U., Bejarano, A., & Berninger, T. (2018). Concepts and applications of foliar spray for microbial inoculants. *Applied Microbiology and Biotechnology, 102*(17), 7265–7282. https://doi.org/10.1007/s00253-018-9173-4

Qadir, M., Quillérou, E., Nangia, V., Murtaza, G., Singh, M., Thomas, R. J., Drechsel, P., & Noble, A. D. (2014). Economics of salt-induced land degradation and restoration. *Natural Resources Forum, 38*(4), 282–295. https://doi.org/10.1111/1477-8947.12054

Rajendran, G., Sing, F., Desai, A. J., & Archana, G. (2008). Enhanced growth and nodulation of pigeon pea by co-inoculation of *Bacillus* strains with *Rhizobium* spp. *Bioresource Technology, 99*(11), 4544–4550. https://doi.org/10.1016/j.biortech.2007.06.057

Ramadoss, D., Lakkineni, V. K., Bose, P., Ali, S., & Annapurna, K. (2013). Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. *SpringerPlus, 2*(1), Article 6. https://doi.org/10.1186/2193-1801-2-6

Romero, F. M., Marina, M., & Pieckenstain, F. L. (2014). The communities of tomato (*Solanum lycopersicum* L.) leaf endophytic bacteria, analyzed by 16S-ribosomal RNA gene pyrosequencing. *FEMS Microbiology Letters, 351*(2), 187–194. https://doi.org/10.1111/1574-6968.12377

Safdar, H., Amin, A., Shafiq, Y., Ali, A., Yasin, R., Shoukat, A., Ui Hussan, M., & Sarwar, M. I. (2019). A review: Impact of salinity on plant growth. *Nature and Science, 17*(1), 34–40. https://doi.org/10.7537/marsnsj170119.06

Salazar-Garcia, G., Balaguera-Lopez, H. E., & Hernandez, J. P. (2022). Effect of plant growth-promoting bacteria *Azospirillum brasilense* on the physiology of radish (*Raphanus sativus* L.) under waterlogging stress. *Agronomy, 12*(3), Article 726. https://doi.org/10.3390/agronomy12030726

Santos, M. S., Nogueira, M. A., & Hungria, M. (2019). Microbial inoculants: Reviewing the past, discussing the present and previewing an outstanding future for the use of beneficial bacteria in agriculture. *AMB Express, 9*(1), Article 32. https://doi.org/10.1186/s13568-019-0932-0

Saravanakumar, D., & Samiyappan, R. (2007). ACC deaminase from *Pseudomonas fluorescens* mediated saline resistance in groundnut (*Arachis hypogaea*) plants. *Journal of Applied Microbiology, 102*(5), 1283–1292. https://doi.org/10.1111/j.1365-2672.2006.03179.x

Sarkar, A., Ghosh, P. K., Pramanik, K., Mitra, S., Soren, T., Pandey, S., Mondal, M. H., & Maiti, T. K. (2018). A halotolerant *Enterobacter* sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. *Research in Microbiology, 169*(1), 20–32. https://doi.org/10.1016/j.resmic.2017.08.005

Shultana, R., Zuan, A. T. K., Naher, U. A., Islam, A. K. M. M., Rana, M. M., Rashid, M. H., Irin, I. J., Islam, S. S., Rim, A. A., & Hasan, A. K. (2022). The PGPR mechanisms of salt stress adaptation and plant growth promotion. *Agronomy, 12*(10), Article 2266. https://doi.org/10.3390/agronomy12102266

Shultana, R., Zuan, A. T. K., Yusop, M. R., Saud, H. M., & El-Shehawi, A. M. (2021). *Bacillus tequilensis* strain 'UPMRB9' improves biochemical attributes and nutrient accumulation in different rice varieties under salinity stress. *PLoS ONE, 16*(7), Article e0260869. https://doi.org/10.1371/journal.pone.0260869

Souza, R., Ambrosini, A., & Passaglia, L. M. P. (2015). Plant growth-promoting bacteria as inoculants in agricultural soils. *Genetics and Molecular Biology, 38*(4), 401–419. https://doi.org/10.1590/S1415-475738420150053

Sun, L., Sun, S., Liu, T., Lei, X., Liu, R., Zhang, J., Dai, S., Li, J., & Ding, Y. (2025). Association analysis of the genomic and functional characteristics of halotolerant *Glutamicibacter endophyticus* J2-5-19 from the rhizosphere of *Suaeda salsa*. *Microorganisms, 13*(1), Article 208. https://doi.org/10.3390/microorganisms13010208

Tanveer, M., & Shabala, S. (2018). Targeting redox regulatory mechanisms for salinity stress tolerance in crops. In D. J. Huang & S. Shabala (Eds.), *Salinity responses and tolerance in plants* (Vol. 1, pp. 213–234). Springer. https://doi.org/10.1007/978-3-319-75671-4_8

Teixeira, J., & Pereira, S. (2007). High salinity and drought act on an organ-dependent manner on potato glutamine synthetase expression and accumulation. *Environmental and Experimental Botany, 60*(1), 121–126. https://doi.org/10.1016/j.envexpbot.2006.09.003

Trejo, A., de-Bashan, L. E., Hartmann, A., Hernandez, J.-P., Rothballer, M., Schmid, M., & Bashan, Y. (2012). Recycling waste debris of immobilized microalgae and plant growth-promoting bacteria from wastewater treatment as a resource to improve fertility of eroded desert soil. *Environmental and Experimental Botany, 75*, 65–73. https://doi.org/10.1016/j.envexpbot.2011.08.007

Türkan, I., & Demiral, T. (2009). Recent developments in understanding salinity tolerance. *Environmental and Experimental Botany, 67*(1), 2–9. https://doi.org/10.1016/j.envexpbot.2009.05.008

Upadhyay, S. K., Singh, J. S., & Singh, D. P. (2011). Exopolysaccharide-producing plant growth-promoting rhizobacteria under salinity condition. *Pedosphere, 21*(2), 214–222. https://doi.org/10.1016/S1002-0160(11)60120-3

van Zelm, E., Zhang, Y., & Testerink, C. (2020). Salt tolerance mechanisms of plants. *Annual Review of Plant Biology, 71*(1), 403–433. https://doi.org/10.1146/annurev-arplant-050718-100005

Vieira, R. F., Ferracini, V. L., Silveira, A. P. D., & Pazianotto, R. A. A. (2021). Improvement of growth of common bean in phosphorus-deficient soils by phosphate-solubilizing and phytohormone-producing bacteria. *Agronomía Colombiana, 39*(3), 372–380. https://doi.org/10.15446/agron.colomb.v39n3.95461

Vinocur, B., & Altman, A. (2005). Recent advances in engineering plant tolerance to abiotic stress: Achievements and limitations. *Current Opinion in Biotechnology, 16*(2), 123–132. https://doi.org/10.1016/j.copbio.2005.02.001

Wisniewski-Dyé, F., Lozano, L., Acosta-Cruz, E., Borland, S., Drogue, B., Prigent-Combaret, C., Rouy, Z., Barbe, V., Herrera, A. M., González, V., & Mavingui, P. (2012). Genome sequence of *Azospirillum brasilense* CBG497 and comparative analyses of *Azospirillum* core and accessory genomes provide insight into niche adaptation. *Genes, 3*(4), 576–602. https://doi.org/10.3390/genes3040576

Wungrampha, S., Joshi, R., Singla-Pareek, S. L., & Pareek, A. (2018). Photosynthesis and salinity: Are these mutually exclusive? *Photosynthetica, 56*, 366–381. https://doi.org/10.1007/s11099-017-0763-7

Yadav, A. K., & Chandra, K. (2014). Mass production and quality control of microbial inoculants. *Proceedings of the Indian National Science Academy, 80*(2), 483–489. https://doi.org/10.16943/ptinsa/2014/v80i2/5

Yang, J., Kloepper, J. W., & Ryu, C.-M. (2009). Rhizosphere bacteria help plants tolerate abiotic stress. *Trends in Plant Science, 14*(1), 1–4. https://doi.org/10.1016/j.tplants.2008.10.004

Zhang, N., Zhao, B., Zhang, H., Weeda, S., Yang, C., Yang, Z., Ren, S., & Guo, Y. (2013). Melatonin promotes water-stress tolerance, lateral root formation, and seed germination in cucumber (*Cucumis sativus* L.). *Journal of Pineal Research, 54*(1), 15–23. https://doi.org/10.1111/j.1600-079X.2012.01015.x

Zhang, Y., Li, D., Zhou, R., Wang, X., Dossa, K., Wang, L., Zhang, Y., Yu, J., Gong, H., Zhang, X., & You, J. (2019). Transcriptome and metabolome analyses of two contrasting sesame genotypes reveal the crucial biological pathways involved in rapid adaptive response to salt stress. *BMC Plant Biology, 19*(1), Article 66. https://doi.org/10.1186/s12870-019-1665-6

Zhu, J.-K. (2001). Plant salt tolerance. *Trends in Plant Science, 6*(2), 66–71. https://doi.org/10.1016/S1360-1385(00)01838-0

Zulfiqar, F., & Ashraf, M. (2021). Nanoparticles potentially mediate salt stress tolerance in plants. *Plant Physiology and Biochemistry, 160*, 257–268. https://doi.org/10.1016/j.plaphy.2021.01.028