

Investigating rhizosphere dynamics and plant-microbe interactions to alleviate environmental stress

Jameel M. AL-KHAYRI^{1*}, Tahir KHAN²

¹Department of Agricultural Biotechnology, College of Agriculture and Food Sciences, King Faisal University, Al-Ahsa 31982, Saudi Arabia; jkhayri@kfu.edu.sa (*corresponding author)

²Bacha Khan University, Department of Botany, Charsadda 24540, Khyber Pakhtunkhwa, Pakistan; tabirbotany123@gmail.com

Abstract

Soil acts as a crucial reservoir for both nutrients and microorganisms, hosting a wide range of microbial communities essential for ecosystem health. Particularly noteworthy are the interactions between plants and these microbes in the rhizosphere, as they actively contribute to sustaining plant well-being and fortifying plants against environmental pressures. Challenges, such as drought and salinity, pose significant threats to agricultural output and overall plant development. Therefore, it is imperative to explore the intricate mechanisms of stress responses to develop strategies to bolster plant resilience. Plant growth-promoting rhizobacteria (PGPR) offer a promising avenue for alleviating stress-induced damage in plants. Recent progress in the understanding of drought stress has shed light on the physiological and biochemical reactions within plants, emphasizing the critical role of abscisic acid (ABA) in stress mitigation. Similarly, advancements in research on salinity tolerance have elucidated the functions of ion transporters and stress signaling proteins. PGPRs play a crucial role in enhancing plant stress resilience through various mechanisms, including the regulation of ethylene levels, enhancement of nutrient absorption, and synthesis of hormones and enzymes. Utilizing the synergistic potential of plant-microbial interactions presents a promising strategy for tackling salinity and drought challenges in agriculture. Furthermore, PGPRs are instrumental in mitigating the effects of organic pollutants and heavy metals via mechanisms such as ACC deaminase activity. Innovative approaches, such as constructed wetland systems, leverage plant-microbial interactions to enhance water quality by purging pollutants.

Keywords: microbial interactions; plant; rhizosphere environment; stress

Introduction

The term "rhizosphere" coined by Lorenz Hiltner (Hiltner, 1904; Hartmann *et al.*, 2008), describes a micro-environment where bacteria, known as bacteriorhiza, actively participate, significantly impacting plant nutrition (Shu and Huang, 2022). The soil environment undergoes continuous fluctuations and dynamic shifts over time. Within this context, there are abundant nutrients and essential elements stored in humus, which support a diverse array of microorganisms. The rhizosphere, the area surrounding plant roots, hosts various organisms, including fungi, bacteria, viruses, actinomycetes, blue-green algae, and protozoa. These

Received: 13 Oct 2024. Received in revised form: 21 Nov 2024. Accepted: 12 Dec 2024. Published online: 20 Dec 2024.

From Volume 49, Issue 1, 2021, Notulae Botanicae Horti Agrobotanici Cluj-Napoca journal uses article numbers in place of the traditional method of continuous pagination through the volume. The journal will continue to appear quarterly, as before, with four annual numbers.

microorganisms play diverse roles, such as decomposing pollutants, maintaining the soil structure, and facilitating the transport of essential nutrients to plants. The root activity profoundly influences the rhizosphere, leading to significant changes. Preserving biodiversity and ecosystem health depends heavily on the richness of microbial communities. Interactions between plants and microbes are vital for ecosystem function. In addition to providing support, water absorption, and nutrient storage, root systems interact closely with different soil microbes. As highlighted by Berg and Smalla (2009), these interactions encompass symbiotic, associative, or chance encounters involving both endophytic and free-living microbes. Symbiotic relationships, such as those between diazotrophs and legumes as well as mycorrhizal fungi, profoundly influence the nutritional and growth dynamics of plants, as emphasized by Brimecombe *et al.* (2007). Plant stress encompasses unforeseen challenges and fluctuations that disrupt essential metabolic functions, potentially leading to harm or illness. These disturbances stem from factors that upset the natural equilibrium. Gaspar *et al.* (2002) observed that plants can respond to environmental changes. Various environmental factors, such as inadequate or excessive nutrients, extreme temperatures, drought, and salinity (Shaddad, 2010) pose obstacles to plant growth and development. The term "stress" originates from the Latin word 'Stringere', which suggests an external force or pressure. In plants, stress refers to external pressures that impede dry matter production during growth, either wholly or partially. Stress refers to unforeseen limitations or alterations that disrupt typical metabolic processes in plants, resulting in illnesses, injuries, or abnormal physiological conditions (Jaleel *et al.*, 2009). Environmental stress and air pollution have significant adverse effects on humans, animals, and plants, with plants being particularly susceptible owing to their immobility, which prevents them from relocating in response to unfavorable conditions, as emphasized by Zhu (2002). Plant stress can be categorized into two primary types, biotic and abiotic, both of which hinder growth and reduce productivity. Biotic stress arises from living organisms, such as pests and diseases, whereas abiotic stress stems from environmental factors, such as water scarcity, high salinity, and extreme temperatures, all of which are widespread and harmful to plants. These stressors induce changes in plant morphology, physiology, and genetics (Aleel *et al.*, 2009). In this study, to investigated the effects of plant growth-promoting rhizobacteria (PGPR) on stress tolerance and bolster plant resilience under challenging environmental conditions.

Advancements in plant drought stress

Drought stress poses a notable challenge in dry and semi-arid agricultural settings, and is emerging as a prominent abiotic obstacle with global ramifications. Its impact on crop yield is profound and significantly jeopardizes global food security. Severe water scarcity can hinder photosynthesis, disrupt metabolic processes, and ultimately lead to plant mortality (Jaleel *et al.*, 2009). Drought stress arises from inadequate rainfall, leading to reduced soil moisture and intensified water scarcity owing to heightened evaporation and transpiration. While plants inherently possess some resilience to drought, the degree of resilience varies among species and even within the same species (Gaspar *et al.*, 2002). Recognized as the primary abiotic challenge confronting crops worldwide, the pervasive occurrence of drought on a global scale poses a significant threat to agricultural output, in terms of both quantity and quality. With the expanding global population and impacts of climate change, drought conditions have escalated worldwide, exacerbating critical situations. This pressure adversely affects crop performance, often resulting in decreased yield (Damghan, 2009). The dynamic nature of drought, encompassing its variability in occurrence, intensity, duration, and timing, along with its interaction with other environmental factors such as salinity and cold temperatures, significantly affects agricultural output (Jaleel *et al.*, 2009). Plants encounter diverse environmental hurdles and adjust to them accordingly. Drought stress triggers a spectrum of physiological and biochemical adjustments in plants, including stomatal closure, halting cellular growth and photosynthesis, heightened respiration, and activation of stress responsive genes. These responses largely stem from the signals induced by soil aridity (Seki *et al.*, 2007). In instances of simultaneous

salt and drought stress, the swift production of the plant hormone abscisic acid is of pivotal importance, greatly aiding the plant's capacity to endure and rebound from these adversities. Hence, it has earned the moniker "stress hormone" (Bray, 2004). The regulation of multiple genes in response to abiotic stress is significantly influenced by the presence of abscisic acid. Additionally, abscisic acid treatment induces the activation of genes sensitive to drought, salt, and cold stress. Therefore, enhancing plant resilience to drought is of significant economic importance. A key objective in advancing strategies is to understand the mechanisms underlying drought resistance. Drought elicits various plant responses, including alterations in gene expression, accumulation of metabolites, such as abscisic acid, and augmentation of osmotically active compounds, such as hydrophilic proteins, oxygen radical-absorbing proteins, and chaperones (Shinozaki *et al.*, 2003).

Advancements in plant salt stress

Primary salinization refers to the natural occurrence of salt in marshland soils or in areas where salt is already present. Some plant species have adapted to saline conditions. In contrast, secondary salinization occurs in soils with initially low salt concentrations, which can become saltier owing to inadequate irrigation practices. Soil salinization is a significant contributor to soil degradation and salinity. Currently, approximately 19.5% of irrigated land and 2.1% of dry-land agricultural areas worldwide are affected by soil salinization (Khan *et al.*, 2018). The increasing prevalence of soil salinity poses a significant challenge in achieving optimal crop yields. As a result, there has been a focus on cultivating plants capable of withstanding salinity-induced stress (Katiyar-Agarwal *et al.*, 2005). Recent progress in rhizosphere research, coupled with a deeper understanding of ion transporter mechanisms and stress-signaling proteins, has significantly enhanced our understanding of how plants maintain ion equilibrium. Substantial research efforts have concentrated on identifying ion transporters and the regulatory pathways implicated in preserving the delicate balance of Na⁺ ions and the cytoplasmic K⁺/Na⁺ ratio (Katiyar-Agarwal *et al.*, 2005). Notably, numerous genes responsive to drought stress are also triggered by salinity stress or exposure to abscisic acid, underscoring the intricate interplay among plant reactions to these environmental stimuli (Shinozaki *et al.*, 2003). Moreover, genetically modified plants engineered for salinity tolerance also exhibit resilience to a range of other stressors including cold, frost, heat, and drought (Katiyar-Agarwal *et al.*, 2005).

Hormones

Hormones play a pivotal role in altering growth patterns to fortify plants against diverse stress factors. A plant's reaction to stress entails a complex interplay among various hormones, their unique response mechanisms, linked genetic networks, and transcription factors.

Plant stress response to abscisic acid (ABA)

Originally known for its growth-inhibiting properties, abscisic acid (ABA) has since been discovered to play various physiological roles in plants. These include the regulation of bud and seed dormancy, leaf and fruit detachment, the promotion of senescence, and the enhancement of stress tolerance. Research indicates that elevated ABA levels facilitate the adaptation of plants, such as tomato, potato, winter wheat, spinach, and arabidopsis to drought or cold conditions. ABA appears to coordinate plant responses to a range of environmental signals, exerting a minor influence on germination, while undergoing significant accumulation during drought stress. This accumulation influences the expression of numerous genes, implying ABA's role of

ABA as a mediator in plant-water communication (Gómez *et al.*, 1988). ABA plays a pivotal role in delineating the genetic pathways that respond to abiotic stresses in plants, distinguishing them into ABA-dependent and ABA-independent pathways. It is noteworthy that there is an intersection between ABA-dependent and ABA-independent regulatory pathways, particularly with respect to drought stress adaptation. Within these regulatory networks, various transcription factors supervise the gene clusters (Buitink *et al.*, 2006).

Subclass III SNF1-related protein kinase 2 (SnRK2s) are essential for regulating signaling and gene expression under drought conditions, particularly in response to osmotic stress caused by abscisic acid (ABA). During osmotic stress, ABA receptors (PYR/PYL/RCAR complexes) inhibit protein phosphatase 2C (PP2C), which removes the inhibition of subclass III SnRK2s. This allows for the activation of these kinases through phosphorylation by B-type Raf-like kinases and GSK3-like kinases independent of ABA. Once activated, subclass III SnRK2s phosphorylate targets, such as ABA-responsive element binding proteins (AREB) and ABA-responsive element binding factors (ABF), leading to the activation of stress-related gene expression. In contrast, subclass I SnRK2s, which do not respond to ABA, are rapidly activated under osmotic stress through ABA-independent pathways. These kinases play a role in mRNA turnover by phosphorylating the mRNA-decapping activator VCS. The activation of subclass I SnRK2s is mediated by B4 Raf-like kinases including RAF18, RAF20, and RAF24. The dashed lines in the diagram indicate the possible pathways that have not yet been confirmed (Soma *et al.*, 2021).

PGPR in mitigating ethylene-induced stress in plants

The presence of rhizosphere bacteria is pivotal in managing the surge in ethylene concentrations in plants during stressful situations, thereby alleviating the detrimental effects of this hormone on the development and growth of plant components, particularly the roots. Plant Growth-Promoting Rhizobacteria (PGPR) modulate ethylene production by releasing deaminase-ACC. As a result, this enzyme indirectly fosters plant growth by reducing stress-induced ethylene levels within the plant (Grichko and Glick, 2001). Plants have the capacity to react to fluctuations in ethylene hormone levels when encountering diverse environmental and biological challenges such as salinity, cold, heat, and heavy metals. Ethylene is generated in soil through biological and non-biological processes (Saghafi *et al.*, 2013). Researchers have explored the potential of various PGPR strains to mitigate the detrimental effects of salinity stress on a range of plant species, including *Arachis hypogaea*, soybeans, rapeseed, tomatoes, corn, lettuce, radishes, and peanuts. Notably, investigations by Shukla *et al.* (2012), yielded significant insights into this domain. Their findings revealed a correlation between enhanced stress resistance in plants and reduced ethylene activity facilitated by the deaminase-ACC enzyme present in diverse bacterial strains. During periods of drought and salinity stress, plants support rhizosphere microorganisms to fortify their defenses. This instigates a complex network of functional interactions orchestrated by PGPR, which shields plants from the deleterious effects of stress, beneficial molecules and activities foster communication with the roots, establishing a vital supportive network that is crucial for plant survival. In the rhizosphere, PGPR directly engages with the roots, bolstering plant growth and secretion through the release of various regulatory molecules. These bacteria amplify their beneficial effects through direct interactions with host plant tissues (Figure 1) (Giauque *et al.*, 2019). Plant Growth-Promoting Rhizobacteria (PGPR), along with Rhizobium bacteria, provide a habitat for various beneficial rhizosphere bacteria such as *Bacillus*, *Pseudomonas aeruginosa*, *Acetobacter*, *Enterobacter*, *Herbaspirillum*, *Azospirillum*, and several unidentified strains, highlighting the extensive microbial diversity within PGPRs (Dobbelaere *et al.*, 2003). PGPRs hold promising potential for enhancing plant growth and fortifying resilience against various stressors through a combination of direct and indirect approaches. They actively engage in crucial processes, such as nitrogen fixation, enhancing nutrient absorption from the growing medium, and synthesizing or emitting secondary metabolites, such as siderophores and ACC deaminase. Additionally, they play a role in

regulating growth hormones such as auxins, cytokinins, and gibberellins. Conversely, the indirect influence of PGPRs on plant growth arises from its ability to mitigate or prevent the detrimental effects of pathogens. Common indirect mechanisms include the secretion of compounds, such as hydrogen cyanide, antibiotics, and enzymes designed to specifically target and degrade pathogen cell walls (Olanrewaju *et al.*, 2017).

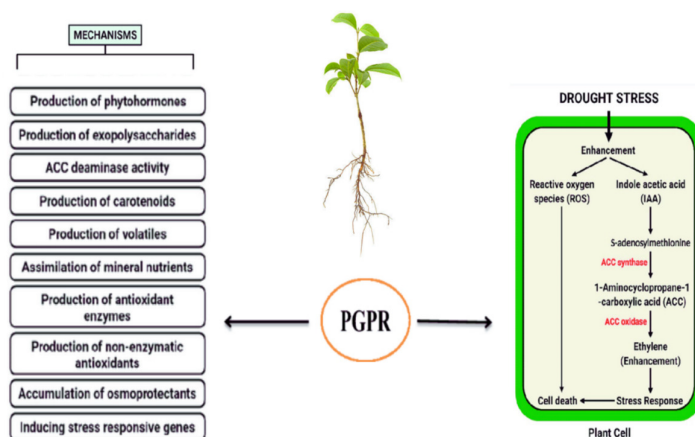


Figure 1. PGPR, which shields plants from the deleterious effects of stress, beneficial molecules and activities foster communication with the roots

Enhancing nitrogen fixation and iron absorption in plants

Nitrogen plays a pivotal role in fostering plant growth as an indispensable element. Nitrogen fixation, wherein atmospheric nitrogen (N_2) is transformed into ammonium (NH_4), is essential for this purpose. Despite the presence of nitrogen in the atmosphere, around seventy-eight percent of it remains unutilized. This element is crucial for the production of amino acids and proteins. Biological nitrogen fixation (BNF) involves an enzymatic reaction catalyzed by nitrogenase, which converts nitrogen into ammonia, a form that soil can use. Nitrogen is a fundamental constituent of nearly all biomolecules such as amino acids in proteins, DNA, RNA, and nucleic acids, and nitrogen fixation is vital for the sustenance of all organisms. Certain organisms within the nitrogen cycle play a pivotal role in maintaining their balance and autotrophs shoulder this responsibility in natural ecosystems. In addition to their contribution to carbon stabilization, green plants also significantly aid nitrogen stabilization (Aasfar *et al.*, 2021). Siderophores appear in four chemical varieties, catecholates, phenolates, hydroxamates, and carboxylates. In soil, iron is commonly present as a trivalent insoluble hydroxide, which poses a challenge for plants to absorb. PGPR secrete small siderophore molecules that are strongly attracted to iron, thereby enhancing its absorption within plant cells (Saha *et al.*, 2016).

ACC deaminase and plant growth hormones

ACC Deaminase is a vital component of Plant Growth-Promoting Rhizobacteria (PGPRs) and serves as a direct mechanism crucial for plant development. Its primary function involves the deactivation of ACC, the precursor of ethylene, while generating ammonia and alpha-ketobutyrate. Elevated levels of ethylene can impede plant growth, potentially leading to plant death. Environmental stressors can intensify ACC synthase and ACC oxidase activities, resulting in increased ethylene levels. PGPRs play a pivotal role in mitigating stress-induced damage to plants by enhancing ACC deaminase activity. This augmentation enables plants to endure adverse conditions better, thereby fostering enhanced resilience and survival (Glick, 2014). The phytohormone

IAA, which is predominantly present in plant-associated bacteria, plays a pivotal role in mediating interactions between plants and bacteria (Luo *et al.*, 2018). Gibberellins are indispensable for facilitating the transportation of metabolites, chloroplast development, and influencing the natural aging process of the leaves. Additionally, they stimulate cell division and contribute to stem cell development (Rizza and Jones, 2019). Its primary function is to enhance root vitality, particularly by promoting the growth of primary and secondary roots, which leads to increased root exudation. Cytokinins are crucial for enhancing vascular development and embryonic growth, and aiding in adaptation to environmental changes and stress management (Hamza and AL-Taey, 2020).

PGPR in mitigating organic pollutants and heavy metals

In addition to organic compounds, heavy metals pose a significant threat to plant health by altering the soil chemistry and physics. Often existing in insoluble salt forms, heavy metals force plants to develop mechanisms to cope with the oxidative stress that they induce (DalCorso *et al.*, 2019). PGPR play a crucial role in ecological balance through various mechanisms, such as nitrogen fixation, nutrient enrichment, suppression of ethylene synthesis, direct synthesis of plant hormones, and elevation of oxygen levels. These bacteria aid in the decomposition of organic pollutants and alleviate their negative effects. They are primarily categorized into rhizosphere bacteria, residing near or on the root surface, and endophytes, which infiltrate the root tissues. Endophytes shielded by roots can protect the host from the harmful effects of pollutants (Lumactud *et al.*, 2016). Plants activate physiological and molecular processes, such as active ion transport, to guide these substances from the roots to cellular vacuoles (Ma *et al.*, 2016). Chemicals such as ethylenediaminetetraacetic acid (EDTA), ethylenediamine-N, N-disuccinic acid (EDDS), and plant growth-promoting bacteria (PGPR) facilitate the transport of heavy metals into vacuoles, thus mitigating their harmful effects (Mishra *et al.*, 2017). This approach has gained recognition for its efficacy in reducing heavy metal concentrations in various plant species. Research indicates that *Bacillus pumilus* (Ma *et al.*, 2016), *Rhodococcus erythropolis* (Liu *et al.*, 2015), *Bradyrhizobium* sp. (Guo and Chi, 2014), as well as *Ralstonia eutropha* and *Chryseobacterium humi* (Moreira *et al.*, 2014), among other strains of plant growth-promoting rhizobacteria (PGPR), have demonstrated this capability. Plants treated with these PGPR strains exhibited a noteworthy decrease in reactive oxygen species (ROS) accumulation and displayed elevated levels of antioxidant enzymes, such as peroxidase (POD), superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX). Further investigations have indicated that plants inoculated with PGPR experience enhancements in photosynthetic pigments, leaf shoot number, and root length (Raklami *et al.*, 2019).

Plant-microbial and PGPR is susceptible to salinity and drought

Salt stress is a significant abiotic factor that can adversely affect plant morphology and physiology by reducing the fresh and dry biomass of the shoots and roots. This is likely due to elevated concentrations of salt ions and changes in water availability (Khan *et al.*, 2018). During prolonged drought periods, these beneficial bacteria release phytohormones, osmolytes, and antioxidants, triggering structural and morphological alterations in the roots that enhance the plant's resilience to stress. Enhanced root development and branching under drought conditions enable deeper soil penetration (Figure 2), facilitating the improved uptake of essential nutrients and moisture by the plant. Through these mechanisms, plants can effectively adapt to adverse environmental conditions and sustain their water and mineral requirements (Misra *et al.*, 2020). The effects of salt stress on maize were evaluated using selective growth responses, osmoregulatory processes, and antioxidant enzyme activity (Khan *et al.*, 2018). Leveraging plant-microbial interactions can yield positive

outcomes for addressing salinity and drought challenges. Plants exhibit robust defense mechanisms against drought and other environmental stresses, particularly through their roots, which display remarkable structural and morphological adaptability. Drought triggers significant alterations in phospholipid makeup in root membranes. Under conditions of water scarcity, many Plant Growth-Promoting Rhizobacteria (PGPR) produce abscisic acid (ABA), a hormone capable of modulating plant responses. Elevated levels of ABA facilitate stomatal closure, decrease leaf transpiration, and consequently, enhance water retention within plants during drought conditions (Vurukonda *et al.*, 2016). PGPR play a crucial role in mitigating the impacts of abiotic stressors, such as drought, salinity, and soil alkalinity, on plant growth (Enebe and Babalola, 2018). Salinity causes two primary challenges in plants: osmotic stress and ionic toxicity. These challenges disrupt various plant physiological processes (Khan *et al.*, 2018). Moreover, PGPR primarily enhance root elasticity, facilitating the penetration of new roots into the soil to access deeper water reservoirs (Koevoets *et al.*, 2016). Furthermore, PGPR play a role in drought resilience by facilitating salt storage within the plant cells through osmotic regulation. Accumulation of various protective substances such as proline, glycine, phenylalanine, organic acids, sugars, and mineral ions, which protect plants from potential oxidative damage (Gagne' -Bourque *et al.*, 2016). Soil salinization poses a significant nonliving challenge and is becoming increasingly menacing on a global scale. This stressor substantially reduces the yield of various crops. Excessive salt concentrations detrimentally affect soil quality, particularly the organic components (Schirawski and Perlin, 2018). Salinization encompasses a spectrum of salts, such as sodium chloride (NaCl), sodium sulfate (Na₂SO₄), magnesium sulfate (MgSO₄), and magnesium chloride (MgCl₂). Among these, NaCl stands out as the most consequential, precipitating heightened salinity levels and inflicting biochemical and physiological harm on plants (Flowers and Colmer, 2015). Although many soil microorganisms can endure high salt concentrations (Table 1), such as *Bacillus*, *Pseudomonas*, *Agrobacterium*, *Enterobacter*, *Klebsiella*, *Streptomyces*, and *Ochromobacterium* species, plants experience significant stress in saline environments, resulting in various detrimental effects. These include diminished photosynthetic activity, restricted nutrient absorption, cell membrane damage, and dehydration, ultimately leading to plant death (Zhang *et al.*, 2018). Generally, PGPR enhance plant salinity tolerance by facilitating the accumulation of osmolytes, augmenting nutrient uptake, fixing nitrogen, solubilizing phosphorus and other vital elements, exhibiting ACC deaminase activity, and synthesizing auxins, siderophores, and exopolysaccharides (Saghafi *et al.*, 2019). Abiotic stresses such as drought and salinity exert significant effects. While selecting stress-resistant species and comprehending their underlying biochemical mechanisms are effective approaches, PGPR can yield the most substantial impact in mitigating plant damage from salinity and drought (Ma *et al.*, 2020).

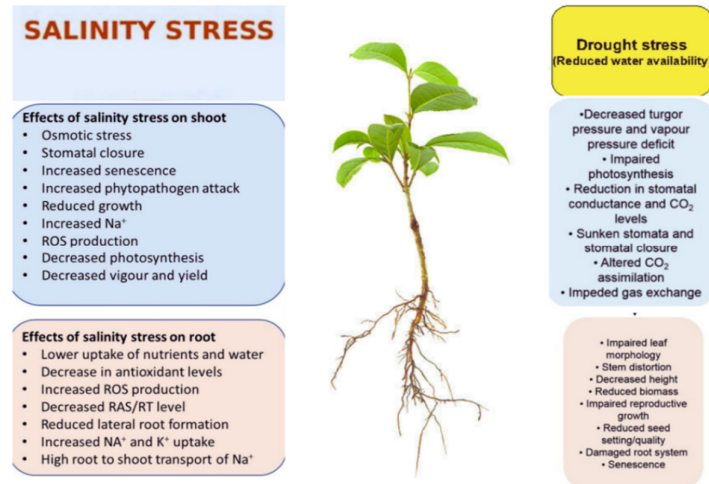


Figure 2. Enhanced root development and branching under salt and drought conditions enable deeper soil penetration, facilitating the improved uptake of essential nutrients and moisture by the plant

Table 1. This indicates that different soil microorganisms can endure different salt concentrations

Plant species	Microorganism	Salinity (mM)	Effect	References
Wheat (<i>Triticum aestivum</i>)	<i>Azotobacter chroococcum</i>	200	Proline and amino acid	(Allaoua <i>et al.</i> , 2016)
Rice (<i>Oryza sativa</i>)	<i>Bacillus and Pseudomonas</i>	Saline soil	Phyostimulation	(Jha and Subramanian, 2016)
Maize (<i>Zea mays</i>)	<i>Azotobacter nigricans</i>	100-200	Enlargement, growth parameters, and germination	(Sagar <i>et al.</i> , 2016)
Millet (<i>Panicum miliaceum</i>)	<i>E. cloacae</i>	100-200	Enhance seed germination and enhanced root and shoot elongation	(Sagar <i>et al.</i> , 2020)
Sorghum (<i>Sorghum bicolor</i>)	<i>Azotobacter salinestris</i>	50	Enhance plant growth, carbohydrate, proline, and macroelements	(Omer <i>et al.</i> , 2016)
Mung bean (<i>Vigna radiata</i>)	<i>Enterobacter cloacae</i>	80	Increase growth parameters, fresh and dry weights	(Bhise <i>et al.</i> , 2016)
Tomato (<i>Solanum lycopersicum</i>)	<i>Azotobacter chroococcum</i>	100	Promoted plant growth	(VanOosten <i>et al.</i> , 2018)
Pea (<i>Pisum sativum</i>)	<i>Bacillus subtilis RbStr_71</i>	10	Enhanced the antioxidant enzymes	(Gupta <i>et al.</i> , 2021)
Chickpea (<i>Cicer arietinum</i>)	<i>Bacillus subtilis</i>	200	Increased the synthesis of photosynthetic pigments and plant biomass	(Abd_Allah <i>et al.</i> , 2018)

Enhancing water quality

Earth possesses abundant water resources; however, only 3% of it is freshwater available globally, leading to approximately three billion people experiencing restricted access to water for their daily needs. The escalation in global temperature has resulted in the depletion of rivers, springs, and freshwater reservoirs on a global scale, rendering many of these water sources unable to sustain diverse ecosystems. This has exacerbated

the challenge of meeting the needs of the population (Carvalho *et al.*, 2017). Consequently, there is a pressing need for innovative strategies for enhancing water reuse and management. Constructed wetland (CW) systems operating on the principles of water rejuvenation and purification have emerged as a promising solution. Plants play a pivotal role in augmenting the water quality by extracting pollutants from water bodies. Rhizobacteria, which facilitate plant growth under adverse conditions, such as drought, salinity, and pollution, contribute to this process by diminishing plant metabolism and alleviating pollutants, particularly heavy substances within the plant (Dhuldhaj and Malik, 2022). Plant Growth-Promoting Rhizobacteria (PGPR) perform various vital functions that effectively mitigate environmental stresses such as salinity, heavy metals, and hydrocarbons. One crucial role involves the production of phytohormones such as 3-indole acetic acid (IAA), abscisic acid (ABA), cytokinins (CKs), and gibberellins (GAs), which are instrumental in regulating plant physiology. Additionally, PGPR exhibits ACC deaminase (ACCD) activity, which reduces ethylene levels while simultaneously activating antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD). Moreover, they regulate ion balance through $\text{Na}^+(\text{K}^+)/\text{H}^+$ pumps and produce exopolysaccharides (EPS). Concurrently, they synthesize osmolytes, such as proline, glycine, and betaine, thus assisting in maintaining protein conformation (Vocciante *et al.*, 2022).

Transcription factors, soil degradation, and phytoremediation

Transcription factors possess the capability to control the expression of multiple target genes by binding to specific sequences within their promoters. The invaluable but limited ecological resources of soil face significant degradation as a result of human activities, such as transportation, urban expansion, and the unlawful disposal of waste (Vocciante and Meshalkin, 2020). Contamination of soil with heavy metals, mineral oils, polycyclic aromatic hydrocarbons, and similar pollutants can have detrimental impacts on ecosystems, natural resources, and human well-being. As a result, remediation of polluted soil and sites is crucial for safeguarding the environment and the health of all organisms. Various approaches have been developed to address water pollution effectively (Puri *et al.*, 2021). This transcriptional regulation mechanism is termed regulon. Examination of stress-induced gene expression has revealed the presence of at least four distinct regulatory systems intended to respond to stress (Nakashima and Yamaguchi-Shinozaki, 2005): DREB, NAC, and ZF-HD regulators operate autonomously from abscisic acid and remain unaffected by either abscisic acid or cold exposure. Conversely, MYC/MYB and AREB (ABF) regulators depend on abscisic acid functionality. Modulating the expression of these regulatory factors has the potential to enhance plant resilience to environmental stressors (Nakashima and Yamaguchi-Shinozaki, 2005). The potential of genetically modified plant species to address soil and water contamination is substantial. However, this technique requires the utilization of raw materials and occasionally involves chemicals, which inevitably impact plants. Thus, phytoremediation is a promising alternative. This is a cost-effective and sustainable method employed to address pollutants while concurrently aiding plant species in optimizing soil and water resources. During this process, plants harness beneficial bacteria to eliminate contaminants, thus mitigating their adverse effects through root secretion. Plant growth-promoting rhizobacteria (PGPR) play a pivotal role in bolstering plant health, particularly under adverse conditions. In agricultural contexts, PGPR serve as valuable allies in mitigating the detrimental effects of abiotic stressors, such as salinity and drought, offering a sustainable substitute for environmentally harmful mineral fertilizers (Conte *et al.*, 2021). Furthermore, biomass obtained through phytoremediation holds the potential for conversion into bioenergy, which not only promotes biodiversity but also aids in soil stabilization (Pedron *et al.*, 2021). A comprehensive understanding of the structural arrangement of the host plant is crucial for investigating phytoremediation processes. Additionally, the significance of root secretions cannot be overstated as they exert a significant influence on the composition of the microbial community (Vives-Peris *et al.*, 2020). Research on *Zea mays* and *Solanum lycopersicum* suggests that these plants exhibit enhanced ability to absorb beneficial and active bacteria through their root secretions.

These investigations highlight the dynamic nature of the rhizosphere, where chemical and physical properties vary depending on microbial communities, plant health, and species diversity. This intricate interplay renders the rhizosphere one of the most complex ecosystems (Phour *et al.*, 2020). Indeed, the host plant employs sophisticated mechanisms to select the most optimal microbiomes, with some studies interpreting this selection process as a result of co-evolution between the plant and its microbial communities. Moreover, a recent study demonstrated that introducing hydrocarbon-contaminated sediments enhanced microbial activity and increased the activity levels of rhizosphere microbial communities (Truyens *et al.*, 2015).

Conclusions

Soil ecosystems are dynamic environments in which a variety of microorganisms play crucial roles in nutrient cycling, maintaining soil health, and supporting plant growth. Challenges such as drought and salinity pose significant hurdles to global agriculture, impacting crop yield and food security. Nevertheless, advancements in understanding plant-microbe interactions, particularly with Plant Growth-Promoting Rhizobacteria (PGPR), offer promising avenues for enhancing plant resilience to stress. Drought stress is a pressing issue that affects agricultural productivity, particularly in dry and semi-arid regions. Delving into the physiological and biochemical responses of plants to drought, including the role of hormones, such as abscisic acid (ABA), provides valuable insights for developing drought tolerant crops. Enhancing resilience against drought involves genetic manipulation, whereas soil salinity poses a major challenge to global crop cultivation. Recent progress in rhizosphere studies has provided insights into how plants regulate ion balance and cope with salt stress. Utilizing PGPR to regulate ion transporters and stress-signaling proteins offers promising pathways to enhance salt tolerance in crops. Ethylene, a plant hormone, regulates various stress responses and plays a crucial role in mitigating ethylene-induced stress by regulating its production through the secretion of the deaminase-ACC enzyme. This mechanism helps mitigate the adverse effects on plant growth and development under stressful conditions. Water scarcity and contamination are significant obstacles for global water resources. Constructed wetland systems and PGPR integration offer innovative solutions for water recycling and purification. PGPR-induced promotion of plant growth and degradation of pollutants contribute to improving water quality and fostering ecosystem sustainability.

Recommendations

Plant root exudates influence microbial communities in the rhizosphere, and these interactions benefit stress resilience. Specific mechanisms of Plant Growth-Promoting Rhizobacteria (PGPR) include phytohormone modulation (e.g., auxins and cytokinins), biofilm formation, and induced systemic resistance (ISR). Recent studies on synthetic biology approaches and microbiome engineering have optimized rhizosphere functions under stress conditions. Details of osmoprotectants, such as proline, trehalose, and glycine betaine, and their roles in maintaining cell turgor under drought conditions. Recent advances in transcriptomics and proteomics have led to identifying drought-tolerant genes. Breeding and genetic engineering efforts for drought tolerance, such as CRISPR-based approaches targeting drought-related genes. Delve deeper into the roles of Salt Overly Sensitive (SOS) pathways and High-Affinity Potassium Transporters (HKTs) in managing salt stress. This study provides examples of halophytes and their salt tolerance mechanisms to develop strategies for salinity-resilient crops. Recommend sustainable agricultural practices such as phytoremediation, biochar application, or using salt-tolerant PGPR to mitigate soil salinity. Explore the interactions between ABA and other hormones such as jasmonic acid (JA), ethylene, salicylic acid (SA), and auxins during stress responses. Molecular pathways involving SnRK2 and other ABA-responsive elements. How exogenous ABA application improves stress resilience in crops is being

tested. Schematic of rhizosphere-microbe interactions. ABA-dependent and ABA-independent stress response pathways Comparative analysis of plant responses to drought and salt stress. Explore the potential of next-generation sequencing (NGS) to unravel complex plant-microbe-soil interactions. Research on multi-stress environments in which drought, salinity, and temperature stresses co-occur. Suggest areas for innovation in PGPR applications, such as bioformulations for specific crops and regions.

Authors' Contributions

Both authors read and approved the final manuscript.

Ethical approval (for researches involving animals or humans)

Not applicable.

Funding

This work was supported by the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia [Project No. KFU242755].

Acknowledgements

This work was supported by the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia [Project No. KFU242755].

Conflict of Interests

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

References

- Aasfar A, Bargaz A, Yaakoubi K, Hilali A, Bennis I, Zeroual Y, Meftah Kadmiri I (2021). Nitrogen fixing *Azotobacter* species as potential soil biological enhancers for crop nutrition and yield stability. *Frontiers in Microbiology* 12:628379. <https://doi.org/10.3389/fmicb.2021.628379>
- Abd_Allah EF, Alqarawi AA, Hashem A, Radhakrishnan R, Al-Huqail AA, Al-Otibi FON, Malik JA, Alharbi RI, Egamberdieva D (2018). Endophytic bacterium *Bacillus subtilis* (BERA 71) improves salt tolerance in chickpea plants by regulating the plant defense mechanisms. *Journal of Plant Interactions* 13:37-44. <https://doi.org/10.1080/17429145.2017.1414321>
- Allaoua S, Hafsa CS, Bilal Y (2016). Growing varieties durum wheat (*Triticum durum*) in response to the effect of osmolytes and inoculation by *Azotobacter chroococcum* under salt stress. *African Journal of Microbiology Research* 10:387-399. <https://doi.org/10.5897/AJMR2015.7723>
- Berg G Smalla K (2009). Plant species and soil type cooperatively shape the structure and function of microbial communities in the rhizosphere. *FEMS Microbiology Ecology* 68:1-13. <https://doi.org/10.1111/j.1574-6941.2009.00654.x>

- Bhise KK, Bhagwat PK, Dandge PB (2016). Plant Growth-Promoting characteristics of salt tolerant *Enterobacter cloacae* strain KBPD and its efficacy in amelioration of salt stress in *Vigna radiata* L. Journal of Plant Growth Regulation 36: 215-226. <https://doi.org/10.1007/s00344-016-9631-0>
- Bray EA (2004). Genes commonly regulated by water-deficit stress in *Arabidopsis thaliana*. Journal of Experimental Botany 55(407):2331-2341. <https://doi.org/10.1093/jxb/erb270>
- Brimecombe MJ, DeLeij FAAM, Lynch JM (2007). Rhizodeposition and microbial populations. In: Pinton R, Varanini Z, Nannipieri P (Eds). The Rhizosphere Biochemistry and Organic Substances at the Soil-Plant Interface. CRC Press: Boca Raton, FL, USA, pp 73-109. <https://doi.org/10.1201/9781420005585.ch3>
- Buitink J, Leger JJ, Guisle I, Vu BL, Wuijle S, Lamirault G, Bars AL, Meur NL, Becker A, Ku`ster H (2006). Transcriptome profiling uncovers metabolic and regulatory processes occurring during the transition from desiccation-sensitive to desiccation-tolerant stages in *Medicago truncatula* seeds. Plant Journal 47(5):735-750. <https://doi.org/10.1111/j.1365-313X.2006.02822.x>
- Carvalho PN, Arias CA, Brix H (2017). Constructed wetlands for water treatment: New developments. Water 9(6):397. <https://doi.org/10.3390/w9060397>
- Conte A, Chiaberge S, Pedron F, Barbaferri M, Petruzzelli G, Vociante M, Franchi E, Pietrini I (2021). Dealing with complex contamination: A novel approach with a combined bio phytoremediation strategy and effective analytical techniques. Journal of Environmental Management 288:112381. <https://doi.org/10.1016/j.jenvman.2021.112381>
- DalCorso G, Fasani E, Manara A, Visioli G, Furini A (2019). Heavy metal pollution: State of the art and innovation in phytoremediation. International Journal of Molecular Sciences 20(14):3412. <https://doi.org/10.3390/ijms20143412>
- Damghan I (2009). Exogenous application of brassinosteroid alleviates drought induced oxidative stress in *Lycopersicon esculentum* L. General and Applied Plant Physiology 35:22-34.
- Dhuldhaj UP, Malik N (2022). Global perspective of phosphate soliloquizing microbes and phosphatase for improvement of soil. Food and Human Health, Cellular, Molecular and Biomedical Reports 2(3):173-186. <https://doi.org/10.55705/cnbr.2022.347523.1048>
- 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>
- Enebe MC, Babalola OO (2018). The influence of plant growth-promoting rhizobacteria in plant tolerance to abiotic stress: A survival strategy. Applied Microbiology and Biotechnology 102(18):7821-7835. <https://doi.org/10.1007/s00253-018-9214-z>
- Flowers TJ, Colmer TD (2015). Plant salt tolerance: Adaptations in halophytes. Annals of Botany 115(3):327-331. <https://doi.org/10.1093/aob/mcu267>
- Gagne´-Bourque F, Bertrand A, Claessens A, Aliferis KA, Jabaji S (2016). Alleviation of drought stress and metabolic changes in timothy (*Phleum pratense* L.) colonized with *Bacillus subtilis* B26. Frontiers of Plant Science 7:584. <https://doi.org/10.3389/fpls.2016.00584>
- Gaspar T, Franck T, Bisbis B, Kevers C, Jouve L, Hausman JF, Dommès J (2002). Concepts in plant stress physiology. Application to plant tissue cultures. Plant Growth Regulation 37(3): 263-285. <https://doi.org/10.1023/A:1020835304842>
- Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research 169(1):30-39. <https://doi.org/10.1016/j.micres.2013.09.009>
- Gómez J, Sánchez-Martínez D, Stiefel V, Rigau J, Puigdoménech P (1988). A gene induced by the plant hormone abscisic acid in response to water stress encodes a glycine rich protein. Nature 334(6179):262-264. <https://doi.org/10.1038/334262a0>
- Grihko VP, Glick BR (2001). Amelioration of flooding stress by ACC deaminase containing plant growth-promoting bacteria. Plant Physiology and Biochemistry 39(1):11e17. [https://doi.org/10.1016/S0981-9428\(00\)01212-2](https://doi.org/10.1016/S0981-9428(00)01212-2)
- Guo J, Chi J (2014). Effect of Cd-tolerant plant growth-promoting rhizobium on plant growth and Cd uptake by *Lolium multiflorum* Lam. and *Glycine max* (L.) Merr. in Cd-contaminated soil. Plant and Soil 375(1):205-214. <https://doi.org/10.1007/s11104-013-1952-1>
- Gupta A, Rai S, Bano A, Khanam A, Sharma S, Pathak N (2021). comparative evaluation of different salt-tolerant plant growth-promoting bacterial isolates in mitigating the induced adverse effect of salinity in *Pisum sativum*.

- Biointerface Research in Applied Chemistry 11:13141–13154.
<https://doi.org/10.33263/BRLAC115.1314113154>
- Hamza OM, AL-Taey DK (2020). A study on the effect of glutamic acid and benzyl adenine application upon growth and yield parameters and active components of two broccoli hybrids. *International Journal of Agriculture and Statistical Science* 16:1163-1167.
- Hartmann A, Rothballer M, Schmid M (2008) Lorenz Hiltner, a pioneer in rhizosphere microbial ecology and soil bacteriology research. *Plant and Soil* 312:7-14. <https://doi.org/10.1007/s11104-007-9514-z>
- Hiltner L (1904) Ueber neuere Erfahrungen und Probleme auf dem Gebiete der Bodenbakteriologie und unter besonderer Berücksichtigung der Grundung und Brache. *Arb. Deut. Landw. Gesell* 98:59-78.
<https://doi.org/10.12691/aees-1-6-1>
- Jaleel CA, Manivannan P, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram R, Panneerselvam R (2009). Drought stress in plants: A review on morphological characteristics and pigments composition. *International Journal of Agriculture and Biology* 11(1):100-105.
- Jha Y, Subramanian RB (2016). Regulation of plant physiology and antioxidant enzymes for alleviating salinity stress by potassium mobilizing bacteria. In: *Potassium Solubilizing Microorganisms for Sustainable Agriculture*; Springer: New Delhi, India, pp 149-162. https://doi.org/10.1007/978-81-322-2776-2_11
- Katiyar-Agarwal S, Verslues P, Zhu JK (2005). Mechanisms of salt tolerance in plants. *Plant nutrition for food security, human health and environmental protection*. 23.
- Khan T, Ullah S, Shuaib M, Alsamadany H, Alzahrani Y, Alharbi N, Shah M, Khan A, Khan I, Hussain F (2018). Effect of naphthyl acetic acid foliar spray on amelioration of salt stress tolerance in maize *Zea mays* L. *Applied Ecology and Environmental Research* 17(2):1817-1834. http://dx.doi.org/10.15666/aeer/1702_18171834
- Koevoets IT, Venema JH, Elzenga JTM, Testerink, C (2016). Roots withstanding the environment: Exploiting root system architecture responses to abiotic stress to improve crop tolerance. *Frontiers of Plant Science* 7:1335.
<https://doi.org/10.3389/fpls.2016.01335>
- Liu W, Wang Q, Wang B, Hou J, Luo Y, Tang C, Franks AE (2015). Plant growth-promoting rhizobacteria enhance the growth and Cd uptake of *Sedum plumbizincicola* in a Cd-contaminated soil. *Journal of Soils and Sediments* 15(5):1191-1199. <https://doi.org/10.1007/s11368-015-1067-9>
- Lumactud R, Shen SY, Lau M, Fulthorpe R (2016). Bacterial endophytes isolated from plants in natural oil seep soils with chronic hydrocarbon contamination. *Frontiers in Microbiology* 7:755. <https://doi.org/10.3389/fmicb.2016.00755>
- Luo J, Zhou JJ, Zhang JZ (2018). Aux/IAA gene family in plants: Molecular structure, regulation, and function. *International Journal of Molecular Sciences* 19(1):259. <https://doi.org/10.3390/ijms19010259>
- Ma Y, Dias MC, Freitas H (2020). Drought and salinity stress responses and microbe-induced tolerance in plants. *Frontiers of Plant Science* 11:591911. <https://doi.org/10.3389/fpls.2020.591911>
- Ma Y, Rajkumar M, Zhang C, Freitas H (2016). Beneficial role of bacterial endophytes in heavy metal phytoremediation. *Journal of Environmental Management* 174:14-25. <https://doi.org/10.1016/j.jenvman.2016.02.047>
- Mishra J, Singh R, Arora NK (2017). Alleviation of heavy metal stress in plants and remediation of soil by rhizosphere microorganisms. *Frontiers in Microbiology* 8:1706. <https://doi.org/10.3389/fmicb.2017.01706>
- Misra V, Solomon S, Mall A, Prajapati C, Ansari MI (2020). Impact of chemical treatments on *Leuconostoc* bacteria from harvested stored cane/stale cane. *Biotechnology Reports* 27:00501. <https://doi.org/10.1016/j.btre.2020.e00501>
- Moreira H, Marques AP, Franco AR, Rangel AO, Castro PM (2014). Phytomanagement of Cd-contaminated soils using maize (*Zea mays* L.) assisted by plant growth-promoting rhizobacteria. *Environmental Science and Pollution Research* 21(16):9742-9753. <https://doi.org/10.1007/s11356-014-2848-1>
- Nakashima K, Yamaguchi-Shinozaki K (2005). Molecular studies on stress-responsive gene expression in Arabidopsis and improvement of stress tolerance in crop plants by regulon biotechnology. *Japan Agricultural Research Quarterly: Japan Agricultural Research Quarterly* 39(4):221229. <https://doi.org/10.6090/jarq.39.221>
- Olanrewaju OS, Glick BR, Babalola OO (2017). Mechanisms of action of plant growth promoting bacteria. *World Journal of Microbiology and Biotechnology* 33(11):1-16. <https://doi.org/10.1007/s11274-017-2364-9>
- Omer AM, Emara HM, Zaghoul RA, Abdel-Monem MO, Dawwam GE (2016). Potential of *Azotobacter Salinestr* as Plant Growth Promoting Rhizobacteria under Saline Stress Conditions. *Research Journal of Pharmaceutical, Biological and Chemical Sciences* 7:2572--2583.

- Pedron F, Grifoni M, Barbaferi M, Petruzzelli G, Rosellini I, Franchi E, Bagatin R, Vocciant M (2017). Applicability of a Freundlich-like model for plant uptake at an industrial contaminated site with a high variable arsenic concentration. *Environments* 4(4):67. <https://doi.org/10.3390/environments4040067>
- Phour M, Sehrawat A, Sindhu SS, Glick BR (2020). Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. *Microbiological Research* 241:126589. <https://doi.org/10.1016/j.micres.2020.126589>
- Pietrelli L, Ferro S, Reverberi AP, Vocciant M (2020). Removal and recovery of heavy metals from tannery sludge subjected to plasma pyro-gasification process. *Journal of Cleaner Production* 273:123166. <https://doi.org/10.1016/j.jclepro.2020.123166>
- Puri N, Gupta A, Mishra A (2021). Recent advances on nano-adsorbents and nano-membranes for the remediation of water. *Journal of Cleaner Production* 322:129051. <https://doi.org/10.1016/j.jclepro.2021.129051>
- Raklami A, Oufdou K, Tahiri AI, Mateos-Naranjo E, Navarro-Torre S, Rodríguez-Llorente ID, Meddich A, Redondo-Gómez S, Pajuelo E (2019). Safe cultivation of *Medicago sativa* in metal-polluted soils from semi-arid regions assisted by heat-and metallo-resistant PGPR. *Microorganisms* 7(7):212. <https://doi.org/10.3390/microorganisms7070212>
- Rizza A, Jones AM (2019). The makings of a gradient: Spatiotemporal distribution of gibberellins in plant development. *Current Opinion in Plant Biology* 47:9-15. <https://doi.org/10.1016/j.pbi.2018.08.001>
- Sagar A, Kuddus M, Singh BP, Labhane NM, Srivastava SPW (2020). Plant growth promotion of millets under abiotic stress using *Enterobacter cloacae* PR10 (KP226575b). *Journal of Indian Botanical Society* 100:30-41. [10.5958/2455-7218.2020.00024.8](https://doi.org/10.5958/2455-7218.2020.00024.8)
- Sagar A, Shukla PK, Ramteke PW (2017). Salt tolerance plant growth promoting bacterium *Azotobacter nigricans* (KP966496) in sustainable maize Production under salt stress. In Proceedings of the XXVItalo–Latin American Congress of Ethnomedicine SILAE, Modena, Italy, pp 11-15.
- Saghafi K, Ahmadi J, Asghar-zadeh A, Esmailizad A (2013). An evaluation of the influence of PGPR on wheat growth indices under saline stress. *Journal of Soil Biology* 1(1): 47-59. <https://doi.org/10.22092/sbj.2013.120920>
- Saha M, Sarkar S, Sarkar B, Sharma BK, Bhattacharjee S, Tribedi P (2016). Microbial siderophores and their potential applications: A review. *Environmental Science and Pollution Research* 23(5):3984-3999. <https://doi.org/10.1007/s11356-015-4294-0>
- Schirawski J, Perlin MH (2018). Plante-microbe interaction 2017: the good, the bad and the diverse. *International Journal of Molecular Sciences* 19(5):1374. <https://doi.org/10.3390/ijms19051374>
- Seki M, Umezawa T, Urano K, Shinozaki K (2007). Regulatory metabolic networks indrought stress responses. *Current Opinion in Plant Biology* 10(3): 296-302. <https://doi.org/10.1016/j.pbi.2007.04.014>
- Shaddad M (2010). Salt tolerance of crop plants. *Journal of Stress Physiology and Biochemistry* 6(3):64-90.
- Shinozaki K, Yamaguchi-Shinozaki K, Seki M (2003). Regulatory network of gene expression in the drought and cold stress responses. *Current Opinion in Plant Biology*, 6(5): 410-417. [https://doi.org/10.1016/s1369-5266\(03\)00092-x](https://doi.org/10.1016/s1369-5266(03)00092-x)
- Shu WS, Huang LN (2022). Microbial diversity in extreme environments. *Nature Reviews Microbiology* 20:219-235. <https://doi.org/10.1038/s41579-021-00648-y>
- Shukla PS, Agarwal PK, Jha B (2011). Improved salinity tolerance of *Arachis hypogaea* (L.) by the interaction of halotolerant plant-growth-promoting rhizobacteria. *Journal of Plant Growth Regulation* 31(2):195-206. <https://doi.org/10.1007/s00344-011-9231-y>
- Soma F, Takahashi F, Yamaguchi-Shinozaki K, Shinozaki K (2021). Cellular phosphorylation signaling and gene expression in drought stress responses: ABA-dependent and ABA-independent regulatory systems. *Plants* 10:756. <https://doi.org/10.3390/plants10040756>.
- Truyens S, Weyens N, Cuypers A, Vangronsveld J (2015). Bacterial seed endophytes: Genera, vertical transmission and interaction with plants. *Environmental Microbiology Reports* 7(1):40-50. <https://doi.org/10.1111/1758-2229.12181>
- VanOosten MJ, Di Stasio E, Cirillo V, Silletti S, Ventorino V, Pepe O, Maggio A (2018). Root inoculation with *Azotobacter chroococcum* 76A enhances tomato plants adaptation to salt stress under low N conditions. *BMC Plant Biology* 18:205. <https://doi.org/10.1186/s12870-018-1411-5>
- Vives-Peris V, de Ollas C, Gómez-Cadenas A, Pérez-Clemente RM (2020). Root exudates: From plant to rhizosphere and beyond. *Plant Cell Reports* 39(1):3-17. <https://doi.org/10.1007/s00299-019-02447-5>

- Vocciante M, Grifoni M, Fusini D, Petruzzelli G, Franchi E (2022). The role of plant growth-promoting rhizobacteria (PGPR) in mitigating plant's environmental stresses. *Applied Sciences* 12(3):1231. <https://doi.org/10.3390/app12031231>
- Vocciante M, Meshalkin V (2020). An accurate inverse model for the detection of leaks in sealed landfills. *Sustainability* 12(14):5598. <https://doi.org/10.3390/su12145598>
- Vurukonda SSKP, Vardharajula S, Shrivastava M, SkZ A (2016). Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. *Microbiological Research* 184:13-24. <https://doi.org/10.1016/j.micres.2015.12.003>
- Zhang S, Fan C, Wang Y, Xia Y, Xiao W, Cui X (2018). Salt-tolerant and plant-growth promoting bacteria isolated from high-yield paddy soil. *Canadian Journal of Microbiology* 64(12): 968-978. <https://doi.org/10.1139/cjm-2017-0571>



The journal offers free, immediate, and unrestricted access to peer-reviewed research and scholarly work. Users are allowed to read, download, copy, distribute, print, search, or link to the full texts of the articles, or use them for any other lawful purpose, without asking prior permission from the publisher or the author.



License - Articles published in *Notulae Botanicae Horti Agrobotanici Cluj-Napoca* are Open-Access, distributed under the terms and conditions of the Creative Commons Attribution (CC BY 4.0) License.
© Articles by the authors; Licensee UASVM and SHST, Cluj-Napoca, Romania. The journal allows the author(s) to hold the copyright/to retain publishing rights without restriction.

Notes:

- **Material disclaimer:** The authors are fully responsible for their work and they hold sole responsibility for the articles published in the journal.
- **Maps and affiliations:** The publisher stay neutral with regard to jurisdictional claims in published maps and institutional affiliations.
- **Responsibilities:** The editors, editorial board and publisher do not assume any responsibility for the article's contents and for the authors' views expressed in their contributions. The statements and opinions published represent the views of the authors or persons to whom they are credited. Publication of research information does not constitute a recommendation or endorsement of products involved.