



Marine and Salt-Tolerant Microorganisms as Promising Plant Growth Promoting Bioinoculants for Plant Stress Mitigation and Sustainable Agriculture



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UTILIZING every square inch of arable land for crop production is essential for ensuring the food and nutritional security of the world's growing population, given the limited amount of arable land and water resources available. Microorganisms possess many bioactive metabolites, but not all microorganisms exhibit this characteristic. Marine microorganisms live in a very complicated habitat and are exposed to extreme conditions; to adapt, they manage to possess, among others, a diverse array of unique secondary metabolites, including alkaloids, terpenoids, polyketides, and quinones. These metabolites exhibit anti-inflammatory, antimicrobial, and anti-tumor properties. Moreover, many marine bacteria exhibit metal tolerance and contribute significantly to the remediation of soil polluted with heavy metals. Biotechnologies can optimize crop output by taking advantage of these bacteria and soil-plant dynamics, which could help establish a new sustainable agriculture framework. In this situation, much research has focused on the complex relationships between plants and soil-dwelling symbiotic microbes. These bacteria play a pivotal role in enhancing the ecological prosperity of plants inside their indigenous environments. This could lead to improved survival and performance of plants in field conditions. Plant growth-promoting microorganisms (PGPMs) play a crucial role in augmenting the synthesis of bioactive secondary metabolites in plants and have the ability to modulate the plant metabolome under diverse environmental stress conditions. Therefore, this review aims to present the influence of microbes, especially marine-derived microbes, on promoting plant growth and altering its metabolome in response to different environmental stressors.

Keywords: Marine Microorganisms, Plant growth promoting microorganisms, Environmental stresses, Salinity, Heavy metals.

1. Introduction

Modern agriculture practices are more directed towards a “green revolution”. There is increasing awareness of the importance of preserving the microbial richness and biodiversity of soil to improve agriculture sustainability (Sandrini et al., 2022). One of the promising solutions to tackle the diverse biotic and abiotic stresses that challenge plant growth is the usage of biological inoculants. These inoculants are considered environmentally safe, sustainable, chemical-free, and cost-effective alternatives to traditional chemical fertilizers, crop-breeding, and genetic engineering options (Baez-Rogelio et al., 2017; Eida et al., 2020). These beneficial biological inoculants, including plant growth-promoting microorganisms (PGPMs), enhance plant resistance or tolerance to diverse stresses. Among the most challenging abiotic stresses are heat, salinity, drought, and heavy metals contamination (Eida et al., 2020). The PGPMs enhance plant growth in many ways, such as

stimulating growth hormone secretion, enhancing nutrient absorption, nitrogen fixation, and providing defense against diseases (Choudhary et al., 2022).

Nevertheless, exploring and identifying new or under-investigated plant growth-promoting resources is necessary to cope with the climate change challenges. In the meantime, a limited number of studies explore the role of marine or salt-tolerant microbes as potential candidate PGPMs in agriculture practices. However, recent studies confirm the potential of these marine inhabitants to increase the plant resistance to several abiotic stresses, including thermal stress (Pérez-Romero et al., 2019; Redondo-Gómez et al., 2021), osmotic stress (Redondo-Gómez et al., 2021; Carreiras, Caçador, & Duarte, 2022) and limited nutrients availability (Valle-Romero et al., 2023). In order to combat the abiotic stresses such as heat, salinity, and heavy metal pollution that threaten the plant in the context of climate change, this review aims to declare the role of PGPMs in stress mitigation and

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highlight the recent successful trials of employing marine or high-salt-derived microbes as bioinoculants to derive attention for this novel PGP resources.

2. Role of PGPMS in mitigating salinity effect

The most damaging abiotic stress in arid and semiarid regions is salt stress, which has a negative effect on crop development and yields (Isayenkov & Maathuis, 2019). The issue of soil salinity has gained significant prominence in recent times and is widely recognized as a critical abiotic component that poses a substantial threat to agricultural productivity (Isayenkov & Maathuis, 2019). According to Sairam and Tyagi (2004), salinity affects 10 million acres of cultivated agricultural land worldwide each year, and by 2050, it is predicted to damage up to 50% of all arable land (Choudhary *et al.*, 2022). This has the physiological effects of decreasing crop output by preventing seed germination, seedling growth, blooming, and fruit set. In salt-influenced soils, plant development is negatively impacted by osmotic stress, ion toxicity, oxidative stress, and ethylene production. According to Qadir *et al.* (2014), the economic yearly costs of crop production losses due to salt-induced soil degradation were estimated to be US\$ 27.3 billion. Utilizing every square inch of land is now necessary because of the growing population and urbanization. A specific effort will be needed to preserve crop output under salt stress because future climate change predictions imply a rising danger of salinization (Turrall, Burke, & Faurès, 2011). The presence of significant amounts of dissolved salts is the primary cause of salinity in the soil. Increased levels of the ions sodium and

chloride in soils cause osmotic stress in plants that results in an ionic imbalance that inhibits a variety of metabolic functions, including photosynthesis, enzyme activity, and nutrient absorption in plant tissues (Sunita *et al.*, 2020).

Salinity significantly impacts microbial populations, leading to notable changes in the biological features of soil and affecting several microbiological activities (Qadir *et al.*, 2014). Applying PGPMS is a significant approach to mitigating the adverse impacts of salt stress on crops. They may directly or indirectly impact the physiology of the host plant and root exudation. Additionally, PGPMS have unique mechanisms that are essential for promoting plant development and coping with salt stress. Such as the secretion of growth hormones (Auxin, cytokinin, gibberellin, and other plant growth hormones), enhanced nutrient absorption, nitrogen fixation, and defense against diseases (Choudhary *et al.*, 2022). Plants produce volatile organic chemicals because of these bacteria. These microorganisms also secrete siderophores, which bind and dissolve iron (Sunita *et al.*, 2020). For example, according to Riyazuddin *et al.* (2020), plants respond to abiotic stressors such as salt by increasing their production of ethylene, a plant stress hormone, which in turn promotes the acceleration of plant maturity. Certain PGPMS can produce an enzyme known as 1-Aminocyclopropane-1-Carboxylate (ACC) deaminase. This enzyme facilitates the degradation of ACC into ammonia and -ketobutyrate. A decrease in the levels of ACC would lead to a decreased concentration of ethylene production since ACC plays a crucial role as a precursor in ethylene biosynthesis (**Fig.1**).

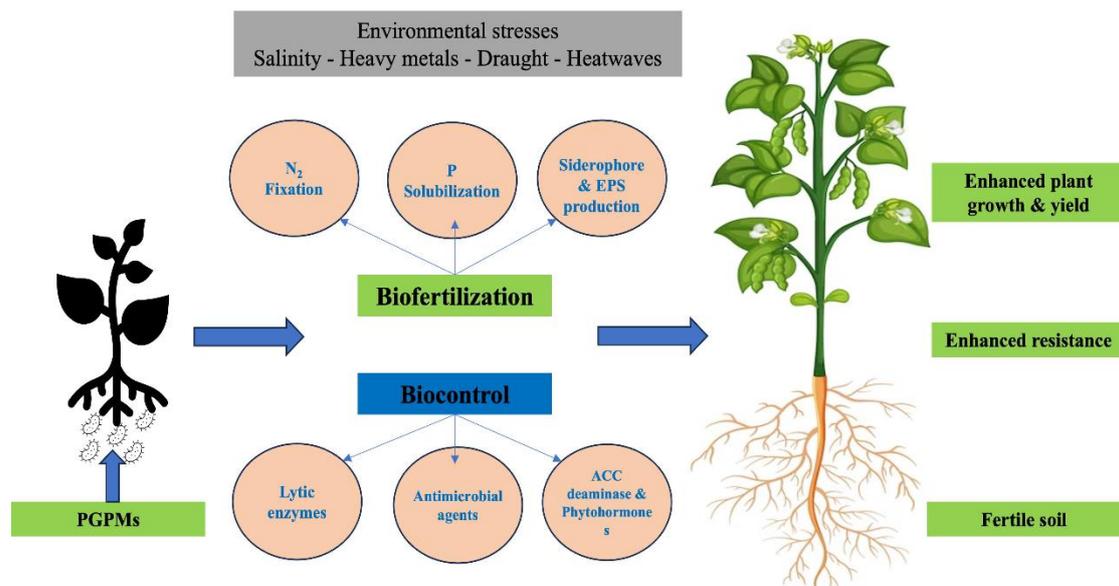


Fig. 1. The role of PGPMS in enhancing plant growth and yield under different environmental stresses for sustainable agriculture.

Furthermore, PGPMs play a crucial role in safeguarding plants against soil-borne diseases. They do this by inhibiting the growth of pathogens in situations with limited nutrients, exerting control over pathogens via the synthesis of biologically active chemicals, producing enzymes that lyse fungal cell walls, and triggering systemic responses in host plants. Furthermore, they mitigate the buildup of proline and lipid peroxidation under circumstances of salt-induced stress.

The existing research on bacteria and their biostimulant activity has predominantly concentrated on strains derived from terrestrial sources, with a particular emphasis on the rhizosphere of crop plants (El-Tarabily et al., 2009; Chen et al., 2018; AbdElgawad et al., 2019). However, there has been a recent surge in the investigation of new functions of bacteria in less-explored environments. Numerous investigations have been undertaken employing organisms derived from saltwater, sediments (Rashad et al., 2015), and the rhizospheres of marsh and mangrove plants (Gong et al., 2018).

Marine microorganisms originating from saline environments have significant promise in agriculture (Oren, 2008). The use of these organisms has the potential to assume a significant function in the biological regulation of foodborne infections and the control of microbes responsible for food spoiling. These challenges are widely recognized as important in the food industry, as highlighted by Essghaier et al. (2014) and Haldar and Sengupta (2016). The high occurrence of salt-affected soils, which poses a significant challenge to agriculture in arid and semi-arid regions, suggests that marine microorganisms may play a crucial role in enhancing plant growth and tolerance to salt stress. In a manner akin to their terrestrial counterparts, some marine strains have been found to possess the ability to produce phytohormones, engage in nitrogen fixation, solubilize phosphate, synthesize siderophores, and mitigate excessive ethylene production through the enzyme ACC deaminase (Rashad et al., 2015). This could lead to improved survival and performance of plants in field conditions (Nabti et al., 2015). For example, prior research has demonstrated that some marine actinobacteria, such as *Streptomyces*, *Isoptericola*, and *Arthrobacter*, can enhance the germination of *Limonium sinensis* plants in soils characterized by different salt levels (Qin et al., 2014). Furthermore, many halotolerant and moderately halophilic microorganisms exhibit metal tolerance and contribute significantly to the remediation of soil polluted with heavy metals (Voica et al., 2016).

The diversity and performance of microbial communities in saline environments are influenced by soil salinity. Natural halophilic bacteria, such as marine bacteria, have many mechanisms to sustain

their active populations in response to elevated salt concentrations. The study conducted by Zhang et al. (2019) revealed a negative correlation between salinity and microbial diversity, indicating a linear decline in the latter. Microorganisms that are capable of thriving in situations with high salinity levels have certain adaptations to cope with osmotic stress. In order to maintain optimal functionality within a given environment, microorganisms often regulate their turgor pressure. Numerous bacteria and archaea have evolved "salt-in and salt-out" strategies, enabling them to withstand high salt concentrations and mitigate the effects of osmotic stressors (Oren, 2002).

The use of marine PGPMs in the process of bioaugmentation has been shown to enhance the plant's ability to withstand and surmount various adversities, such as nutritional deficiency (Valle-Romero et al., 2023), osmotic pressure (Carreiras et al., 2022), heat and severe stress conditions (Redondo-Gómez et al., 2021). Despite studies demonstrating the potential uses of halotolerant plant growth-promoting bacteria (PGPB) as efficient agents for biocontrol and biostimulation (Tirry et al., 2018), it is crucial to note that the majority of these agents frequently exhibit protective capabilities against either abiotic or biotic stressors, but not both at the same time. However, soil and plants are frequently exposed to a variety of stresses. Utilizing a single strain of microorganisms does not facilitate the activation of all conceivable mechanisms that promote growth. Therefore, to harness all potential traits, the adoption of PGPMs consortia is becoming more prevalent in agricultural practices and is currently a subject of research interest (Redondo-Gómez et al., 2021).

2.1. Increasing nutrient uptake

Nutritional imbalance in plants under salt stress inhibits their development and production. Rhizosphere-associated PGPMs modify the root architecture and improve nutrient absorption, maintaining the health of the host plant. The roots can absorb more nutrients and water and can adapt to stressful situations because of the enhanced root system. Additionally, PGPMs improve the availability of nutrients by solubilizing phosphate and nitrogen-fixing bacteria (Choudhary et al., 2018). Organic acids are secreted by P-solubilizing bacteria, which lowers soil pH. Phosphate conjugate bases become more acidic and are more soluble when the pH is reduced (Puenta et al., 2004). Plant salt stress resistance may be positively impacted by nitrogen-fixing capacity.

Furthermore, stress-tolerant rhizobia strains may support legume plants in maintaining their yield and N fixation levels. Rhizobium bacteria that can withstand salt are more effective in fostering plant

development in salty environments. By enhancing nodulation, leghaemoglobin content, and nitrogenase activity and maintaining adequate nutritional levels, inoculation of PGPMs may reduce salt stress (Abd-Alla *et al.*, 2019). In salt-affected soils, PGPMs also improve micro and macronutrient availability and sustain soil fertility (Hafez *et al.*, 2021).

2.2. Phytohormones production

According to Egamberdieva *et al.* (2009), the modulation of hormone release, such as indole acetic acid (IAA), gibberellins (GA), abscisic acid (ABA), and other hormones, by PGPMs enhances root development and enhances nutrient absorption in plants exposed to stressful situations. Khan *et al.* (2019) reported that the endophytic bacteria *Curtobacterium* sp. SAK1 has the potential to mitigate salt stress in soybean plants through the regulation of many physiological processes. These include the modulation of indole-3-acetic acid (IAA), abscisic acid (ABA), siderophore, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase production. In situations characterized by heightened stress levels, bacteria that can produce ACC deaminase may facilitate the conversion of ACC into ammonia and -ketobutyrate. This enzymatic activity results in a reduction in the overall quantity of ethylene present. A study conducted by Ji *et al.* (2020) showed that the introduction of salt-tolerant *Glutamicibacter* sp. YD01 to rice plants resulted in the regulation of plant ethylene production, ACC content, ACC oxidase activity, and K⁺ acquisition. This intervention ultimately enhanced the plant ability to withstand salt stress. Shahid *et al.* (2021) reported that using salt-tolerant *Kosakonia sacchari* improved the mungbean plant's performance.

Additionally, this particular strain exhibited plant growth-promoting characteristics, such as ACC deaminase activity. The levels of Na⁺/K⁺ ions and the extent of membrane damage were both seen to be reduced. The study conducted by Kang *et al.* (2019) showed that *Leclercia adecarboxylata* MO1, a bacterium with halotolerant properties, exhibited a substantial production of indole-3-acetic acid. Additionally, the presence of the *acdS* gene, responsible for producing ACC deaminase, was detected. Moreover, these bacteria significantly enhanced the synthesis of organic acids and sugars, providing a protective mechanism against salt-induced stress.

2.3. Antioxidant enzymes activation

Plants exposed to abiotic stressors, such as salt stress, exhibit an excessive production of reactive oxygen species (ROS). This overproduction of ROS adversely affects the fluidity of the plant's membranes, deactivates proteins attached to the membranes, causes DNA damage, hinders protein

synthesis, and inhibits the activity of enzymes. Kim *et al.* (2014) found that the use of PGPMs resulted in an enhancement of the antioxidative enzymatic activity of catalase (CAT), peroxidase (PO), superoxide dismutase (SOD), and ascorbate peroxidase (APX) in plants. According to Islam *et al.* (2016), the presence of PGPMs in conjunction with antioxidant enzymes facilitates the accumulation of osmolytes and salt within plant cells. Moreover, PGPMs have a crucial role in modulating the functioning of antioxidant enzymes and facilitating the specific absorption of essential ions such as sodium (Na⁺), potassium (K⁺), and calcium (Ca²⁺). This mechanism aids in the maintenance of a balanced ratio of potassium to sodium (K⁺/Na⁺) within plant cells. Rojas-Tapias *et al.* (2012) reported that introducing PGPMs into maize plants increased the K⁺/Na⁺ ratio when exposed to salt stress. This effect was attributed to the enhanced exclusion of Na⁺ ions and increased absorption of K⁺ ions. Additionally, the inoculation of PGPMs led to elevated levels of polyphenols and chlorophyll while reducing the accumulation of proline in the leaves.

2.4. Synthesis of osmolytes

Osmolytes, including proline, alanine, glycine, glutamic acid, serine, threonine, and aspartate, in addition to potassium cations, are synthesized by microbes intracellularly as tiny organic molecules. According to Kumar *et al.* (2020), osmolytes play a vital role in facilitating the survival of microorganisms in the presence of salt stress through the regulation of cell turgor. PGPMs can induce the accumulation of osmolytes within the cytoplasm of plant cells, hence functioning as a mechanism to maintain osmotic equilibrium in the face of stress caused by salt. According to Suprasanna *et al.* (2016), the predominant osmolytes present in plants include sugars, sugar alcohols, glycine, betaine, proline, and glutamate. Furthermore, existing documentation supports the role of these osmolytes as molecular chaperones, which play a crucial role in preserving the structural integrity of proteins and augmenting diverse enzymatic functions.

2.5. Production of Exopolysaccharides (EPS)

Under stress situations, such as high salinity and limited water availability, PGPMs exhibit the formation of biofilms composed of extracellular polymers. Biofilms serve as a protective coating around cells, aiding their survival during stress periods. The study conducted by Ansari *et al.* (2019) investigated the effects of *Bacillus pumilus* FAB10, a biofilm-forming bacterium, on the development of wheat plants and its ability to alter plant physiological characteristics and antioxidant enzyme levels under circumstances of salt stress. The application of EPS-producing bacteria has been

shown to protect plant roots against salt stress by forming a defensive barrier composed of EPS (Awad et al., 2012). The EPS functional groups have the ability to form complexes with Na⁺ ions, impeding or limiting the entry of Na⁺ ions into the root tissue of plants from the surrounding soil (Afridi et al., 2019). Several bacterial species, including *Bacillus* and *Pseudomonas*, have been observed to promote the growth of wheat, mungbean (Mahmood et al., 2016), and soybean (Kasotia et al., 2016) under conditions of salt-induced-stress. It has been demonstrated that bacteria capable of producing EPS enhance plant growth and improve salt-affected soils physical structure by promoting soil aggregation. The inoculation of plants with EPS-producing bacteria has been observed to lead to increased resistance to water and salinity stress due to improvements in soil structure (Alami et al., 2000). EPS also have a notable impact on augmenting water availability and increasing the absorption of nutrients (such as nitrogen, phosphorus, potassium, and iron) from the soil when subjected to salt stress conditions (Etesami & Beattie, 2018). Awad et al. (2012) conducted a greenhouse study wherein they noticed a significant increase in the dry weights of both the roots and shoots with the introduction of *Azotobacter chroococcum*, a bacterium known for its ability to produce EPS. Furthermore, a significant increase was observed in chlorophyll a, chlorophyll b, and carotenoid concentrations. Chu et al. (2019) conducted a study that showcased the ability of the *Pseudomonas* PS01 strain, which generates salt-tolerant EPS, to modulate stress tolerance-related genes in *Arabidopsis thaliana*.

3. Role of PGPMs in mitigating heavy metals (HM) effect

The accumulation of HMs in soil inhibits plant root and shoot growth and alters the soil ecosystem, affecting signal and nutrient exchange and reducing crop yield (Desale et al., 2014). HMs also interfere with CO₂ assimilation in plants by disturbing chloroplast ultrastructure, interrupting the electron transport chain, and decreasing stomatal conductance (Huihui et al., 2020). Moreover, a high concentration of HM ions in the cytosol affects cellular redox homeostasis and causes oxidative stress by generating reactive oxygen species (ROS), which is toxic to plant cells (Ahmad et al., 2015; Sunil et al., 2019). Additionally, HMs pollute the human food chain and lead to adverse health diseases such as cancer, Parkinson's disease, Alzheimer's disease, and atherosclerosis (Muszynska et al., 2015; Shahid et al., 2021).

Phytoremediation is a promising alternative and cost-effective plant-based technique for remediating metal-polluted soils (Ma et al., 2016). However, global climate changes limiting the growth and performance of plants negatively impact plant

adaptation (Rajkumar et al., 2013). Therefore, halotolerant and moderately halophilic bacteria exhibit metal tolerance and contribute significantly to the remediation of soil polluted with HMs, thus offering a promising solution to this problem (Voica et al., 2016). They can adapt to HM-contaminated environments by altering metabolism as a strategy against metal-induced stress (Argudín et al., 2019; Mathivanan et al., 2021). In addition, they revealed inducible genomic responses to stressful levels of HMs present in the environment (Voica et al., 2016). Moreover, bacteria produce siderophores (an iron-chelating substance with low molecular mass), which enhance mobility and reduce the bioavailability of metals and their subsequent removal from soil (Ojuederie et al., 2017). Numerous investigations have addressed the bacterial mechanisms of promoting plant growth in response to HMs. These mechanisms include sequestration, production of metal chelators, precipitation, and enzymatic detoxification (Ojuederie et al., 2017).

Halophytes-associated microbes showed plant growth-promoting capacities. For instance, *Halobacillus* and *Halomonas* strains are promising candidates as plant growth-promoting halophiles (PGPH) in phytoremediation of metal-polluted saline soils by maintaining a favorable chemical composition of the rhizosphere, and thus promoting the growth of *Sesuvium portulacastrum* roots (Desale et al., 2014; Voica et al., 2016). A previous study reported the role of *Pseudomonas citronellolis* SLP6 in enhancing the Cu uptake in roots and phytoremediation efficiency of *Helianthus annuus* in Cu-contaminated saline soils (Silambarasan et al., 2020). A further study reported that *Pseudomonas fluorescens* can promote the growth of *Sedum alfredii* under the stress of Zn and Cd by producing indole-3-acetic acid (IAA) and improving plant Cd absorption through regulating expression and transporting genes of Cd (Chen et al., 2017). Additionally, *Kocuria flava* AB402 and *Bacillus vietnamensis* AB403, arsenic (As) resistant halophilic bacterial strains isolated from mangrove rhizosphere, were decreased as uptake and accumulation in rice seedlings (Mallick et al., 2018). Additionally, PGPH can condition the soil through metabolic activities such as producing metal chelators and organic acids that affect metal solubility, and simultaneously reducing the phytotoxicity of HM-contaminated soil (Desale et al., 2014). Rhizosphere-halotolerant bacteria isolated from HMs-contaminated sites showed plant growth-promoting characteristics, including biofilm formation, nitrogen fixation, siderophores, and IAA in *Spartina maritima* plants (Mesa et al., 2015).

4. Role of PGPMs in mitigating drought effect

Drought is a restrictive ecological factor for the growth of plants and one of the normal phenomena

that influence agricultural production. During drought times, there is a reduction in the soil water potential with a subsequent decrease in plant water potential. Also, water shortage results in an extreme decrease in the electron transport chain (ETC), which raises the photooxidation of plant tissue (Mittler, 2017). Consequently, the activity of Rubisco (EC 4.1.1.39-ribulose-bisphosphate carboxylase) is reduced, and the photosystem II (PSII) membrane complex is damaged, suppressing photosynthetic activity. Therefore, a significant photoprotective response resulting in the dispersal of excess heat is known as the non-photochemical quenching (NPQ) of chlorophyll fluorescence (Sohbat, 2022). Plants also show a sequence of biochemical and molecular machines in reply to drought stress. One of these machines is the initiation of ROS production, resulting in peroxidation, impairing the function of cells, and causing oxidative damage. Therefore, the comeback of plants to drought is a defining factor in preserving atmosphere–soil–plant balance. The plant response to water stress is complicated and includes the management of the expression of genes and their incorporation with hormones.

Researchers propose that bacteria have machines to alleviate the impacts of water stress, promoting more noteworthy development in plants. The known mechanisms comprise a change in growth rate and architecture, root-to-shoot phenotypic change, water conservation, protection of plant cells, hydraulic conductivity, and integration of phytohormones modulation, in addition to some metabolites and stress-prompted enzymatic machines (Bittencourt *et al.*, 2023).

4.1. Bacterial Phytohormones

Promoting plant growth through beneficial microorganisms is mainly related to a complex network of plant hormones vital for development, growth, and responses to abiotic and biotic stimuli (Dodd *et al.*, 2010). Some bacteria can produce and modulate different hormonal groups related to alternations in the location, signaling of hormones, and concentration, and accordingly influencing their equilibrium in the plant (Dodd *et al.*, 2010; Pantoja-Guerra *et al.*, 2023).

One of the best-known hormones is Auxin, which exhibits several described functions, including differentiation, expansion, and cell division. For example, the activity of auxin encourages tubers and seeds germination, increases the development rate of root and xylem, controls the process of vegetative growth, initiates the formation of adventitious and lateral roots, facilitates the responses to gravity, flowering, and light, and affects the formation of pigments and several metabolites to struggle the hard conditions (Spaepen *et al.*, 2014). PGPMs control the auxin

balance and thus alter root growth rates (Lima *et al.*, 2020).

Variations in biochemistry and root anatomy facilitated by phytohormones are one of the familiar actions of microbes on agroecosystems of crops (Etesami & Beattie, 2018; Lima *et al.*, 2020; Pantoja-Guerra *et al.*, 2023). Furthermore, their effects are essential in raising water availability under environmental shortages in case of low water potential. In addition, the enhancement of water influx includes alternation in the organization manner of cortical and epidermal systems of vascular root tissue that moderate the hydraulic conductivity of the root system (Mohammadi Alagoz *et al.*, 2022). Moreover, the auxin pathway signaling initiates electrogenic transmembrane V-type H⁺-ATPase pumps and P-type H⁺-ATPase that facilitate nutrient transport (Canellas *et al.*, 2002). Additionally, the activity of the P-type pump can acidify the apoplast microenvironment near the meristematic tip of the root, which is responsible for tissue, cell, and root axis expansion (Dünser & Kleine-Vehn, 2015). Thus, bacterial inoculum controls balance and auxin signaling, encouraging plant growth under proper water accessibility, or reducing the harmful effects of water shortage on plant development and growth.

Consequently, there is a reduction in ACC concentration outside the cell. The plant can then exude external and internal ACC to maintain the balance. Reduction in ACC results in reduced ethylene, and thus initiating plant growth even in drought conditions (Gamalero & Glick, 2015). Bacteria that produce these enzymes make the plant more resistant to abiotic and biotic stresses (Gamalero & Glick, 2015). Several research demonstrated that bacterial inoculation with the ability to synthesize ACC deaminase is a tremendous promoter of plant growth during drought stress (Gamalero & Glick, 2015; Yasmin *et al.*, 2022).

Mockevičiūtė *et al.* (2023) tried to improve the tolerance of plants to drought through exogenous treatment with stress-protecting compounds. They evaluated the influence of plant probiotics, proline, and calcium on winter wheat in response to drought. They stated that all investigated compounds enhanced the drought tolerance of the plant. ProbioHumus + Ca ProbioHumus exhibited the highest impact on keeping the relative leaf water content (RWC) and growth parameters near those of irrigated plants. They prolonged and decreased the ethylene emission stimulation in leaves during drought. Seedlings treated with ProbioHumus + Ca and ProbioHumus had a considerably lower grade of membrane damage prompted by ROS. Molecular research of drought-responsive genes displayed lower Probiotics + Ca-treated plants vs Ca expressions. This research

displayed that using Ca in combination with probiotics can trigger defense responses compensating for the hostile impacts of drought stress.

In a study by Admassie et al. (2022), they isolated 60 strains of bacteria from pepper in southeast Ethiopia. Pepper seeds inoculated with four designated bacteria that are resistant to drought were evaluated for their effect in the reduction of drought stress using the greenhouse; the supplemented plants showed 41–79.6% and 23.6–52.8% higher root and shoot lengths, respectively, comparing with the uninoculated plants. Their study confirmed that the tested bacteria isolated from endophytes and the rhizosphere of pepper developed on water-scarce lands could mitigate drought stress in crop plants.

Yang et al. (2021) investigated the in vivo effect of adding four bacterial consortiums (SPMX) (*Paenibacillus amylolyticus*, *Xanthomonas retroflexus*, *Microbacterium oxydans*, and *Stenotrophomonas rhizophila*) on *Arabidopsis* plants during drought. They found that SPMX curiously enhanced the plant's survival after 21-day exposure to drought, showing promising characteristics of the inoculated consortium, realizing prompted drought tolerance. Moreover, they displayed that adding the bacterial consortium aided in stabilizing the structure and diversity of root-accompanying microbiomes, possibly benefiting the health of plants exposed to drought.

4.2. Exopolysaccharides production

Forming EPS is a strategy to adhere to surfaces, survive in adverse conditions, and grow. Moreover, they are vital to form and maintain the architecture of the biofilm, nutrient absorption, and water retention in harsh environments (Poli et al., 2011). Therefore, bacteria synthesizing EPS are essential for promoting plant growth under drought stress as this action increases water retention capacity (Ojuederie et al., 2019).

Research has displayed that bacteria from *Azospirillum*, *Pseudomonas*, and *Bacillus*

can secrete EPS under drought conditions (Ghosh et al., 2019; Ojuederie et al., 2019). These polymers can perform as emulsifiers, and therefore, moderate changes caused by ROS. Bacteria-inoculated plants can accumulate amino acids, sugars, proline, and protein and increase leaf area and biomass (Khan & Bano, 2019).

A recent study by Mahreen et al. (2023) investigated using eight drought-tolerant bacteria to biocontrol drought stress in rice. They reported that the inoculated bacterial consortium (*Bacillus cereus* NM-6; *Brucella haematophilum* NM-4 and *Bacillus subtilis* NM-2) enhanced surface area, vigor index, and seedling growth.

4.3. Volatile organic compounds

The PGPMs yield volatile metabolites, increasing development, plant growth, crop productivity, photosynthesis, and iron uptake. These compounds help plants overcome different diseases. For example, 2,3-butanediol and 2-pentylfuran, 3-hydroxy-2-butanone play an essential role in the development and plant growth (Carlson et al., 2020). These compounds control the closing of stomata and resistance to stress to ensure plant development and growth under drought stress conditions (Ilyas et al., 2020). The produced bacterial volatile prompts tolerance to drought stress in the accompanying plants by prompting ROS scavengers' gene expression and formation.

4.4. Osmoregulation

PGPMs can form osmolytes that can act synergistically with osmolytes formed by plants (such as proline, trehalose, soluble sugars, and glycine-betaine), act as osmoprotectants, and stop the damage of cells triggered by drought (Ozturk et al., 2021). Consequently, the aggregation of the formed osmolytes in plants can increase the tolerance to water deficiency, confer membrane stability, and stop electrolyte leakage. Moreover, plants' oxidative damage could be prevented by proline (Hayat et al., 2012). For example, Sziderics et al. (Sziderics et al., 2007) showed that inoculation of pepper plants by *Bacillus* spp. and *Arthrobacter* sp. raised synthesis and accumulation of proline.

4.5. Encapsulation of PGPBs

Diverse research has revealed that PGPB inhabitants are extremely decreased after direct supplementation into the soil in harsh conditions, causing a loss of effectiveness and biological activity (Mendoza-Labrador et al., 2021; Yang et al., 2009). Therefore, using a protective means by trapping bacteria inside a coating is a significant challenge. Different research on encapsulation has explored drought stress, indicating the method's effectiveness for dehydration problems, and improving the protection of cells for protecting plants from drought. The hydrogels formed of polysaccharides, such as cellulose, chitosan, and starch, can absorb and hold a vast amount of water, showing natural abundance, biodegradability, and biocompatibility, which can be applied in agricultural systems for the improvement of soil texture, structure, water retention, and density (Saberri Risch et al., 2021).

5. Role of PGPMs in mitigating heatwave effect

According to the World Meteorological Organization, a heatwave is defined as a prolonged episode, for five days or longer, of increased maximum temperature by five degrees Celsius above the average maximum temperature (World

Meteorological Organization, 2016). Heatwave incidents are anticipated to become more frequent and severe in the next decades due to climate change (Masson-Delmotte *et al.*, 2021). Therefore, innovative solutions are needed to counteract the drastic effects of heat. Among the promising solutions is the usage of marine rhizobacteria bioinoculants. A recent study conducted on the grapevine, one of the most economically important agricultural crops (OIV, 2022), demonstrated the positive impact of bioaugmentation of grapevine plants with marine rhizobacteria (Carreiras *et al.*, 2023). The study included the exposure of grapevine plants to heatwave treatment (42/38 °C day/night) for five successive days. The plants were grown under these conditions (25/21 °C day/night) as a control. The light intensity and humidity were adjusted at 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and $70 \pm 5\%$, respectively. The plants were irrigated every two days. These conditions were set to cope with the widely accepted definition of heatwave simulation (Beniston *et al.*, 2004; Parente *et al.*, 2018; Carreiras *et al.*, 2020).

Interestingly, the plants supplemented with marine rhizobacteria consortia demonstrated significantly higher photoprotection and membrane stability in comparison to the control group. Furthermore, the marine bacterial consortium ameliorated the oxidative stress notably. The exact mechanism of these positive impacts has yet to be defined. However, the overall impact of marine consortia induced either tolerance or resistance to heatwave effects based on the marine consortium members' composition (Carreiras *et al.*, 2023).

6. Next-generation sequencing of PGPMs for more knowledge-oriented biotechnological applications

Nowadays, genomic studies have facilitated a more in-depth analysis of the plant growth-promoting potential of isolated bacterial strains. Furthermore, it improves our understanding of the molecular basis of these beneficial traits (Meena *et al.*, 2017). Next-generation sequencing provides a complete picture of a bacterial strain genes profile and pinpoints its biotechnological potential. In recent years, NGS has been conducted to investigate the genome of many plant growth-promoting *Bacillus* and *Pseudomonas* spp members (Joshi & Chitanand, 2020; Olanrewaju *et al.*, 2021). A recent study conducted by Iqbal *et al.* (2023) on 72 bacterial strains isolated originally from saline-sodic soil or lakes demonstrated practically that nineteen strains exhibited several *in vitro* plant growth-promoting traits, including phosphate solubilization, indole three acetic acid, and lytic enzymes production, and siderophore synthesis.

Moreover, these strains were found to possess biofilm formation capabilities and antibacterial

activities. However, the genome mining of a representative strain (*Bacillus paralicheniformis* strain ES-1) revealed that it encodes genes that function in phosphate solubilization and siderophore production, along with several other beneficial genes associated with nitrogen fixation, chitinase production, hydrogen sulfate synthesis, chemotaxis, and motility (Iqbal *et al.*, 2023). Therefore, genomic studies provide more resolution to identify the wide potential of promising bacterial strains. Indeed, combining *in vitro* and genomic studies helps pinpoint the most effective plant growth-promoting strains for future sustainable agriculture.

On the other hand, NGS on DNA samples extracted from the plant-growing soil or rhizosphere was adopted to explore the microbial communities living in association with the plant. This strategy helps identify the dominant species and their spatial distribution (Alawiye & Babalola, 2019). Moreover, combining the different omics data derived from genomics, transcriptomics, proteomics, and metabolomics studies conducted on the plant rhizosphere facilitates the identification of functional genes. The identification of these genes is essential for future biotechnological manipulations and the generation of climate-resistant varieties to cope with the expected climate changes (Li & Yan, 2020). For example, the clustered, regularly interspaced short palindromic repeats (CRISPR/Cas9) gene editing approach has been recently adopted to generate knockout non-transgenic plants and mutated microbes. This kind of research helps understand the molecular basis of stress tolerance and host-symbiont interactions (Levy *et al.*, 2018; Khatabi *et al.*, 2019; Sandrini *et al.*, 2022).

7. PGPMs consortium and synthetic communities

Selecting a potent sole strain as an inoculant is a key component of the beneficial agricultural utilization of microbial bio-stimulants (Bradáčová *et al.*, 2019). However, in particular situations and under definite stresses, single-strain bio-inocula lack the desired performance in natural habitats because it fails to successfully battle with native soil microflora (Elkoca *et al.*, 2010). This may have resulted from poor inoculum quality, low indigenous colonization percentage, and low survival rates (Khan *et al.*, 2022). As a result, there is an increasing urge to employ microbial consortia products (MCPs), which are constructed from genetically heterogenous collections of compatible microbial strains that interact with one another cooperatively through various mechanisms of action to offer more improved nutrition to plants that enhance plant survival and development in a variety of habitats (Lopez-Cervantes & Thorpe, 2013; Bradáčová *et al.*, 2019). According to Bradáčová *et al.* (2019), The idea behind MCPs

relies on the hypothesis that under different environmental circumstances, different participants of the inoculated microbial communities are exclusively triggered by rhizosphere signals as well as the host plant's ecophysiological reactions, which demonstrate their advantageous impact on plant development.

Marine PGPMs have unique stress resistance qualities since they can tolerate and cope with a broad array of pressures, temperatures, high salt content, pH, and variations in water levels (Pajuelo et al., 2021). The biological augmentation of plants with these marine PGPMs assists plants in enduring several environmental obstacles (Albdaiwi et al., 2019). From the previous point of view, in order to evoke all prospective traits through the activation of all possible growth-promoting pathways, the implementation of PGPMs consortia is the practical current option (Carreiras et al., 2023). Manasa et al. (2021) described using a microbial consortium comprised of two compatible powerful *Bacillus* isolates obtained from marine water and the rhizosphere of the medicinal plant *Coscinium fenestratum*. The consortium members were recognized as the rhizosphere's isolate, *Bacillus mojavensis*, and the marine isolate, *Bacillus cereus*. Both isolates showed their contribution to enhancing sorghum, one of the most significant grain crops, in terms of development, productivity, and iron content. The number of leaves and their areas, the weights of roots, shoots, and leaves, and the total yield of sorghum all rose dramatically as a result of the consortium augmentation in comparison to the effect of each sole strain. Additionally, the biofortification improved the iron content up to 97%, which is of great influence as the inaccessibility of iron is frequently charged for the low sorghum yield.

Furthermore, since the conventional cultivating media only recover less than 10 percent of the microbiota associated with plants, the enrichment of PGPMs is frequently hampered by the absence of specified culture media customized to certain bacterial strains. A high-throughput technique known as "culturomics" is used to meticulously cultivate and identify strains or species in a given sample by supplementing the culture media with particular compounds from the native niche and definite incubation conditions. Compared with the metagenomic characterization of complex microbial communities, this technique was viewed as an alternative path (Sarhan et al., 2019). By using this technique, constructed consortiums known as synthetic microbial communities (SynComs) can be created by choosing 2-4 strains whose "core Genome" emphasizes all the necessary features to create an effective population (Marín et al., 2021). Similarly, two separate bacterial collections were used in an experiment based on

this method for the bioaugmentation of metal stress on *Mesembryanthemum crystallinum*. The main sources of these two collections were the rhizosphere and tissues of *M. crystallinum*, a halophyte on the Mediterranean coasts with a nutraceutical characteristic. (Flores-Duarte et al., 2023). Halotolerant rhizosphere bacteria linked to *M. crystallinum* were believed to assist plants in facing adverse conditions, such as hypersalinity (Mahmood et al., 2019).

Conclusion

The utilization of bioinoculants in agricultural practices offers a potential resolution to the issues associated with the overreliance on chemical fertilizers and pesticides. The bioinoculant process using PGPM is a viable and environmentally friendly approach that positively impacts agricultural output. This method enhances the availability of essential nutrients to plants, boosts their resilience against living organisms and environmental factors, improves soil quality and fertility, and aids in combating harmful diseases. Marine and salt-tolerant PGPMs are a wonderful tool for achieving the goals of sustainable agriculture since they can survive in salty environments, but their structure and composition are only just beginning to be understood. Additional efforts should be allocated toward understanding the stress mitigation processes and popularizing the achievements of marine PGPM applications among governmental entities, agricultural practitioners, and industrial manufacturers to attain food security goals.

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الكائنات البحرية الدقيقة والمقاومة للملوحة كمحفزات حيوية واعدة لنمو النبات لتخفيف الإجهاد النباتي ولزراعة مستدامة

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إن استغلال كل بوصة مربعة من الأراضي الصالحة للزراعة لإنتاج المحاصيل الزراعية أصبح أمراً ضرورياً لضمان الأمن الغذائي لسكان العالم المتزايدين، نظراً للكمية المحدودة من الأراضي الصالحة للزراعة وموارد المياه المتاحة. تمتلك الكائنات الحية الدقيقة العديد من المواد النشطة بيولوجياً، ولكن ليس كل الكائنات الحية الدقيقة تظهر هذه الخاصية. تعيش الكائنات الحية الدقيقة البحرية في بيئة معقدة للغاية وتتعرض لظروف قاسية؛ ولكي تتكيف مع هذه الظروف، يقوموا بإنتاج مجموعة متنوعة من المواد الثانوية الفريدة، بما في ذلك الفلويات، والتيربينويدات، والبوليكيتيدات، والكينونات، من بين أشياء أخرى. تظهر هذه المواد خصائص مضادة للالتهابات ومضادة للميكروبات ومضادة للأورام. علاوة على ذلك، فإن عدداً كبيراً من البكتيريا البحرية يظهر قدرة على تحمل المعادن ويساهم بشكل كبير في معالجة التربة الملوثة بالمعادن الثقيلة. يمكن للتكنولوجيا الحيوية تحسين إنتاج المحاصيل من خلال الاستفادة من هذه البكتيريا وديناميكيات التربة والنباتات، وهو ما يمكن أن يساعد في إنشاء إطار زراعي جديد مستدام. في هذه الحالة، ركزت الكثير من الأبحاث على العلاقات التكافلية المعقدة بين النباتات والميكروبات التي تعيش في التربة. وتلعب هذه البكتيريا دوراً محورياً في تعزيز الازدهار البيئي للنباتات داخل بيئاتها الأصلية. وهذا يمكن أن يؤدي إلى تحسين بقاء وأداء النباتات في الظروف الميدانية. تلعب الكائنات الحية الدقيقة المعززة لنمو النبات (PGPMs) دوراً حاسماً في زيادة تخليق المواد الثانوية النشطة بيولوجياً في النباتات ولديها القدرة على تعديل التمثيل الغذائي للنبات في ظل ظروف الإجهاد البيئي المتنوعة. لهذا يهدف هذا البحث المرجعي الي عرض تأثير الميكروبات، وخاصة الميكروبات من البيئة البحرية، على تعزيز نمو النبات وتغيير أبيضه كاستجابة للضغوطات البيئية المختلفة.