



The Role of PGPB-Microalgae interaction in Alleviating Salt Stress in Plants

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Abstract

Plant development and yield are severely hampered by climate change. Plants are very prone to a variety of abiotic stressors during growth, making them susceptible to destruction which can reduce the productivity by 20–60%. These stresses generate reactive oxygen species (ROS), which damage lipids, proteins, and nucleic acids. Microalgae and plant growth-promoting bacteria (PGPB) are remarkably effective at reducing the effects of salt stress and promoting plant growth, thereby increasing agricultural yield, and helping ensure global food security. Through a variety of mechanisms, including the production of phytohormones, 1-aminocyclopropane-1-carboxylic acid deaminase, exopolysaccharide, siderophores, hydrogen cyanide, extracellular polymeric substances, volatile organic compounds, and modulation of antioxidants defense machinery under abiotic stresses promote plant growth after inoculation of PGPB and microalgae. These microorganisms also maintain ion homeostasis, offer osmotic balance, stimulate genes that respond to salt and drought, rewire the metabolism, modify the transcription of ion transporter genes, and more. To counteract the negative consequences of salinity stress, this study summarizes the effects of PGPB- microalgae along with a tentative protective mechanism during salinity stress for sustainable agriculture.

Introduction

A major challenge for agriculture is to accomplish the food demand of the increasing global population, which is currently growing at higher rate. There are various stresses, responsible for lowering the productivity of various crops [53]. Salinity is one of the major abiotic stresses which significantly reduce crop productivity. The deposition of mineral salts such as NaCl, Na₂SO₄, Na₂CO₃, MgSO₄, NaHCO₃, CaCO₃ and CaSO₄, is a major characteristic of saline soils [31]. Currently, 1125 million hectares of land around the world are affected by salinity, out of which 76 million hectares are due to human-induced salinization. The human-induced salinization activities are mining, industrial management, and high irrigation. There is about 20% of the agricultural area is highly affected by high salinity and this percentage is growing constantly [89, 113].

Agricultural practices such as excessive use of fertilizers, pesticides, and fungicides; unsustainable land use; and

inadequate irrigation can result in salinization of the soil [42]. Additionally, applying fertilizers with high potassium and sodium contents can, under some circumstances, result in the buildup of these salts and induce soil degradation [31]. Limited rainfall and high temperatures also encourage excessive evapo-transpiration which results in an increase in the salinity of the top layers of the soil [4]. Electrical Conductivity measurements give the salinity in the soil, the permissible limit is <0.7 dS/m. A salinity level >3.0 dS/m is assumed to be a high and stressor that can heavily affect soil productivity. Salinity has a multidimensional impact on plants which significantly reduces agricultural output including seed germination, photosynthesis, antioxidants, membrane transport, and ethylene production. Exposure to high salt (NaCl) concentrations around the root zone increases osmotic stress and further generates ion toxicity. Osmotic stress affects water uptake, seed germination, cell elongation leaf development, quiescent lateral bud development, lateral branching, photosynthesis rate, nutrient uptake and translocation from root to shoot, interrupting the supply of carbohydrates to the meristematic regions, and exerts a negative impact on the overall growth of the plant. The high salinity causes an inflow of Na⁺ and Cl⁻ into the cellular compartment which as a result causes an osmotic imbalance

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in plant cells [42], on the other hand, the high concentration of Na^+ also inhibits the absorption of K^+ which is an essential component for plant growth and development. High salinity initiates the accumulation of ROS in the biological components which consequently causes oxidative damage to various biomolecules [50]. Additionally, under salinity stress, photosystem II activity is reduced, which decreases photosynthetic efficiency [49]. Furthermore, vegetative and reproductive growth of plants are negatively impacted by a decrease in photosynthetic rate caused by salinity, which can also delay flowering, reduce fertility, and lead to decreased yield. Overall, from the stage of seed germination to seed development, salinity has a detrimental effect on the physiological and biochemical activities of the plant [108].

However, to recover saline soils, several types of physicochemical approaches are frequently used, including phytoremediation, microbial remediation, and conventional breeding methods, as well as leaching (which involves ponding the soil continuously or intermittently, sprinkling it, and eventually drying it out) and drainage (which involves adding soil amendments like gypsum). The physicochemical methods are unsustainable as they produce environmental pollution. Microbial remediation is considered a cost-effective, non-polluting, energy-saving, and widely applicable method for soil reclamation. Microbial remediation of saline soil is especially needing a certain type of halo tolerant plant growth-promoting bacteria (PGPB) and cyanobacteria such as *Scytonema* sp., *Nostoc* sp., and *Anabaena* sp. The microbes used in the remediation can be both endophytes and exophytes. Endophytes are a type of PGPB that reside inside their host cell and play remarkable success in enhancing the agricultural productivity of saline soils. Microorganisms that reside endophytically or exophytically have a great potential impact on the plant stress response [110]. These microbes can boost plant growth and their stress response by a variety of mechanisms such as nitrogen fixation, mineral solubilization, phytohormone synthesis, and release of siderophores (metal-chelating compounds) [60], [95]; [76]. Other genera of PGPB such as *Bacillus* sp., *Azotobacter* sp. and *Pseudomonas* sp. can also be very beneficial microorganisms to promote plant tolerance against saline conditions by releasing these extracellular compounds which function by the stimulation of genes related to stress, osmolytes, and antioxidant enzymes [53, 115]. Besides the release of the protecting compound to the surroundings, PGPB can also solubilize the metallic compounds and synthesize other plant hormone parameters. Hence, they are widely used worldwide for their characteristics for sustainable agriculture to minimize chemical pesticides and fertilizers over the last several decades [48, 61, 90]. Under salt stress, PGPB along with a variety of microorganisms can offer their host plants several advantages such as encouraging plant development, improving soil fertility, eliminating excess salt from plant

tissues, phosphate solubilization, nitrogen fixation, and phytohormones synthesis [93, 96], [110]; [38, 119]. A proper formulation of these factors must be added to the soil to boost their viability and performance. Cyanobacteria, which are important phyllosphere and rhizosphere components, respond quickly to environmental stresses, reclaiming salt-affected desertified land and promoting vegetation cover. [66, 72, 88–91].

This review discusses the current state of knowledge about the various mechanisms used by PGPB and cyanobacteria to overcome the negative effects of salinity on plants and increase the productivity of saline soils. Numerous articles, which are considered in this review, demonstrated that bacterial and microalgal association boost plant susceptibility and releases various compounds which alleviate the tolerance level of its host in salty environments.

Effect of Salinity on the Various Components of Phyllosphere and Rhizosphere

Cell Membrane Properties

The salinity is essential for multiple biological functions; however, it is quite problematic if it is higher than the threshold values. Generally, there is a huge alteration in the composition of the cell wall of the organisms under high salinity. It can destroy the membrane's integrity by influencing the lipid metabolism [57]. However, the overexpression of receptor-like protein kinase genes (*OsRPK1*) plays an important role in maintaining the plasma membrane's H^+ -ATPase activity under such circumstances. Moreover, other mechanism like enforcement of cell wall by lignification, can also be adopted to tackle the saline environment. Lignin provides extra integrity to the membrane and mechanically reinforces the cell wall. There have been reports of the impact of lignin accumulation on salt tolerance in a variety of crops, including tomato, wheat, and soybean [47]. Along with the reinforcement of the cell wall, other types of pathways are also activated such as the induction of the monogalactosyl diacylglycerol synthase enzyme which maintains the integrity of the thylakoid membrane in thylakoids. High salinity can also damage the integrity by elevating the ROS levels in cell which is generally counteract by the expression of bacterial *acdS* gene by inhibiting the gene expression responsible for ROS production to prevent cellular damage [22]. High salinity results in the osmotic imbalance in micro-environment which is usually tackled by the mobilization of the aquaporins in the cell wall. Under salt stress, the expression of aquaporins along with the tonoplast intrinsic proteins (TIPs) and plasma membrane intrinsic proteins (PIPs) is highly under-expressed [35]. Aquaporins are the member of the family of major intrinsic proteins (MIP). It assists plants to

absorb water from the soil and maintain their roots' hydraulic conductivity. Astonishingly, the role of PGPB becomes quite important in such conditions as they can nullify the effect of salinity and can over-express the aquaporins in such conditions. In doing so, they restore the plant-water relationships. For instance, it was discovered in a study that *Azospirillum brasilense* boosted the expression of the gene *HvPIP2;1* in barley, improving plant-water relationships along with salinity tolerance [118]. In another study, *Pantoea agglomerata* increased the expression of the gene *PIP2;1* in maize and enhanced plant growth in saline environments [55]. PGPBs, such as *Bacillus*, *Pseudomonas*, and *Azospirillum*, are also involved in multiple plant hormone synthesis which directly influences the expression of the Aquaporins. Aquaporin intrinsic membrane proteins are currently well characterized, although only PIPs have been documented to be expressed by specific PGPB during salt stress [57, 88]. Hence, the PGPB are the pioneer components that positively control the expression of certain genes which are essential for the normal functioning of plants. As discussed earlier, under high salinity, the absorption of water and other essential elements is downgraded; however, the PGPB can restore such activities by over-expressing such pathways.

G- proteins and Ligands

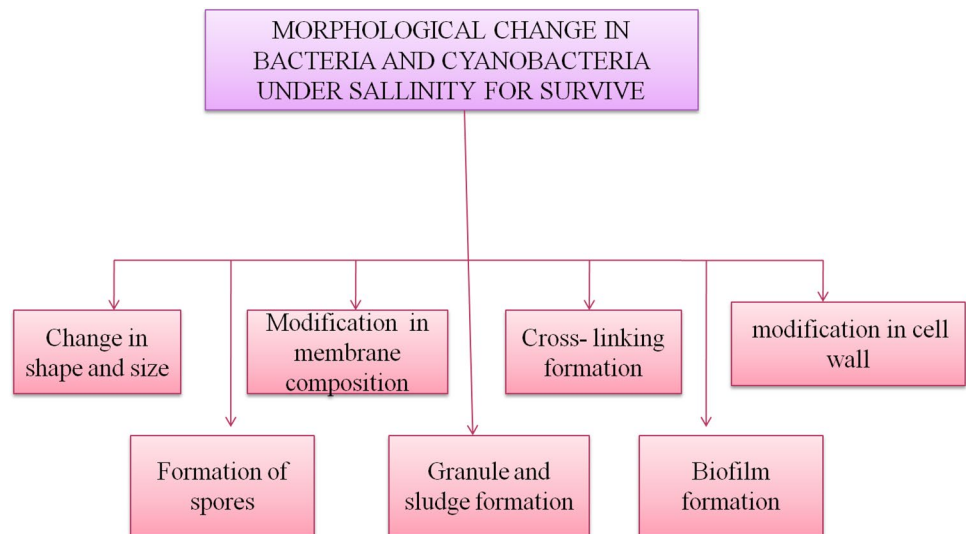
The plant's local environment is formed by the multi-dimensional interaction of various microbial population, which includes bacteria and cyanobacteria, to mitigate the effects of salinity stress. This interaction majorly involves the GPCR-mediated signal transduction. GPCRs are signal transduction pathways most bacteria and cyanobacteria in the phyllosphere/rhizosphere use to detect and respond to salt stress. GPCRs on the surface of plant cells are bound by ligands such as glycine betaine, sucrose, and nodulation factors, which activate G proteins and change the expression of genes linked to the stress response. Some of the major microbes living in the phyllosphere and rhizosphere that contain GPCRs and G-proteins are *B. subtilis*, *Synechocystis* sp. PCC 6803, *Nostoc* sp. PCC 7120, *Salinibacter ruber*, and *Synechocystis* sp. PCC 6803 Canfora et al. [13]. Under salt stress, these microorganisms produce suitable solutes such as glycine betaine, sucrose, and glucosylglycerol, which bind to GPCRs and trigger downstream signaling pathways. Signal transduction in response to salt stress involves calmodulin, annexin, and members of the Rab family of GTPase proteins in addition to secondary messengers such as calcium ions, ROS, inositol phosphate, and phytohormones. These signaling molecules coordinate the cellular reactions of plants and associated phyllosphere and rhizosphere microbes to salt stress. *Bacillus subtilis*, a soil bacterium that can withstand mild salt stress, is another illustration of a bacterial species that synthesizes G-proteins in salinity

[87]. A GPCR in the bacterium known as McpC interacts with glycine betaine, another suitable solute that the bacterium accumulates under salt stress. CheA is a G protein that McpC activates to control the bacterium's chemotaxis towards sources of glycine betaine [42]. A cyanobacterium, *Synechocystis* sp. PCC 6803, which can adapt to a variety of salt concentrations, also expresses G-proteins in high salinity. It has a GPCR called Sre1 that interacts with the compatible solute sucrose, which the cyanobacterium produces when it is under salinity stress [87, 91]. *Nostoc* sp. PCC 7120, a cyanobacterium that forms symbiotic relationships with plants and fungi, is another illustration of a cyanobacterial species that makes G-proteins in salinity. It has a GPCR termed NodQ that binds to nodulation factors, which are signaling molecules made by *rhizobia* bacteria and responsible for causing legumes to develop root nodules [31]. The major function of the G-protein expression is to enhance the symbiosis and nitrogen fixation in which the NodQ plays an important role in activating the G protein NodP. PGPB are essential for improving plants' ability to withstand salt. Through the employment of specialized transporters, PGPB actively pumps out of plant cells, reducing an accumulation of harmful ions and reducing the harm that salinity stress causes [51]. The general health and stress tolerance of the plant are influenced by the interactions with bacteria, cyanobacteria, and plants within the phyllosphere and rhizosphere. Microorganisms in the phyllosphere/rhizosphere promote plants in adjusting to and overcoming salt stress through their interactions and signaling pathways, eventually encouraging plant growth and survival. The interactions among microbes, GPCRs, signaling pathways, and PGPB within the phyllosphere and rhizosphere are crucial for mitigating the effects of salt stress and preserving plant health under demanding environmental circumstances.

Morphological Modifications

The microbes adopt various types of methodologies to combat the abiotic stresses. As it is a well-known fact that the microbes are very crucial for the behavior of the plant species as well as their response towards the environmental factor, it is very considerate to discuss the overall morphological adaptation of the microbes to sustain its activities under salinity stress. Besides retaining its ability and functionality, microbes can also secure the activity of its host under such adverse condition. Microbes are susceptible to morphological alterations brought on by salinity stress, including modifications to cell size, shape, membrane composition, and cell wall composition. These modifications can assist microorganisms in resisting osmotic pressure and preserving their cellular processes. Under salinity stress, some bacteria and cyanobacteria can produce spores, which are latent, hardy entities that can endure extreme circumstances (see Fig. 1).

Fig. 1 Morphological modification in microorganism under salinity stress



Spores are shielded from damage and desiccation by a thick layer of peptidoglycan and proteins [40, 53]. One such microbe is *Bacillus subtilis* which can produce endospores in the presence of high salt concentrations. These endospore-forming bacteria can form beneficial associations with plants and can enhance their growth and production by the mechanism of nitrogen fixation, phosphate solubilization, and plant growth promotion. Another filamentous cyanobacterium that can fix nitrogen enhance plant growth and withstand salinity is *Nostoc*. It can also synthesize heterocyst, which are specialized cells for nitrogen fixation [63].

Under salinity stress, some bacteria and cyanobacteria can alter the morphology of their cells, growing longer or more spherical (See Fig. 1). According to Tufail et al. [102], and Verma et al., [106], this may have an impact on the surface-to-volume ratio, which in turn affects how they exchange water and other substances with the environment. Gram-negative and halophilic, *Halomonas elongate* can thrive in salinities as high as 25%. Depending on the salinity of the medium, it can change the size and length of its cells. It can develop long filaments under high salinity and small rods under low salinity. Due to their survival capacity in salinity conditions, they form various compounds, which help in plant growth and protection [114]. A marine cyanobacteria, *Synechococcus* sp. PCC 7002 can withstand salinities up to 3.5 M NaCl, by altering the proportion of peptidoglycan in its cell wall, it can control its morphological characteristics. Its cell width increases, and its peptidoglycan layer is thicker under conditions of low salinity, whereas in conditions of high salinity, the latter is thinner [108]. A filamentous freshwater cyanobacterium known as *Coleofasciculus chthonoplastes* can survive in salt concentrations as high as 1.5 M NaCl. It can modify the composition and arrangement of its gas vesicles and thylakoid membranes to change its cell shape and ultrastructure. It possesses fewer and more

distributed gas vesicles and thylakoids in low salinity, while more compact thylakoids and gas vesicles in high salinity [99]. Therefore, these microbes can be very efficient in reducing the salinity stress in their host. One such example is the release of promoting factors synthesized by the *Synechococcus* sp. PCC 7002 and *Coleofasciculus chthonoplastes* cyanobacteria which help to improve the productivity of many plants. These symbionts also release certain signaling compounds which can be enacted to assemble a more diverse microbiome around their host. Under salinity stress, both bacteria and cyanobacteria can alter the structure and fluidity of their phospholipids, produce more hopanoids (sterol-like molecules), and incorporate compatible solutes into their membrane, such as glycine, betaine, proline, trehalose ectoine. These changes may aid the bacteria in preserving the stability and integrity of their membranes [43]. Under salinity stress, micro-organism can modify their cell walls by enhancing the cross-linking of peptidoglycan, resulting in the synthesis of more teichoic acids (polymers of glycerol or ribitol), and increasing the amounts of lipopolysaccharides (LPS) in their outer membrane. These modifications can make the bacterium more stiff and able to withstand osmotic shock [109]. In conditions of salinity, *Chlorogleopsis* PCC 6912, *Phormidium uncinatum*, *Gleocapsa* sp., and *Nostoc commune* develop extracellular sheaths that serve as water reservoirs, absorbents, and barriers against desiccation and salinity [77]. Hence, by various mechanisms, these microbes release various compounds which enhance plant growth under abiotic stresses.

Role of Microbial Extracellular Compounds in Mitigating Salt Stress

The mechanism of the tolerance differs significantly in the environment. There are two types of organisms based on

their adaptability to salt stress: Halophytes and glycophytes. Glycophytes which comprise most plant species, cannot survive high salinity. In such plants, the tolerance adaptation comes due to their symbionts like microalgae, fungi, and bacteria. These microbes release certain extracellular substances which function as the osmotic balancer around the plant cell, hence, improving the plant productivity in such conditions [31, 67]. Through several mechanisms including osmotic adjustment, phytohormones synthesis, free radical protection, and the synthesis of extracellular polymeric substances (EPSs), PGPB and cyanobacteria can significantly increase salt tolerance in plants [19]. *Nostoc kihlmani* and *Anabaena cylindrica* produce EPS and enhance soil structure and increased growth of wheat plant [27]. Ansari et al. [5] demonstrated that *Bacillus pumilus* strain FAB10 inoculation in salinity increased EPS production, due to EPS production biofilm are developed around the root surface and enhance salt tolerance property of wheat plant. In one of the studies, it was found that extracellular products released by *Scytonema hofmanni* can significantly improve the development and metabolic activities of *Yerua* PA rice seedlings under high NaCl concentrations. Gibberellin-like

compounds may be present in the cyanobacterial extracellular products and could neutralize the negative effects of salt stress [80]. Similarly, *Chroococcidiopsis* sp., *Anabaena* sp., *N. muscorum*, *Hapalosiphon* sp., and other cyanobacterial species produce growth hormones, vitamins, and peptides that help wheat plants thrive under salinity [33, 41]. The mechanisms of mitigation of salt stress in plants by these microbial floras are depicted in Fig. 2. A more elaborate discussion is presented in the further subsections.

Role of Microbial Compounds

Microbial Release of Cell Signaling Compounds

PGPB also releases certain extracellular compounds which help to recruit all the essential components around its host which are important for the plant in surviving high salinity stress. IAA is believed to be one such signaling compound. It is a naturally occurring phytohormone found in plants and algae that many bacteria can also produce and release. In the algal–bacterial co-cultivation system, *C. sorokiniana*

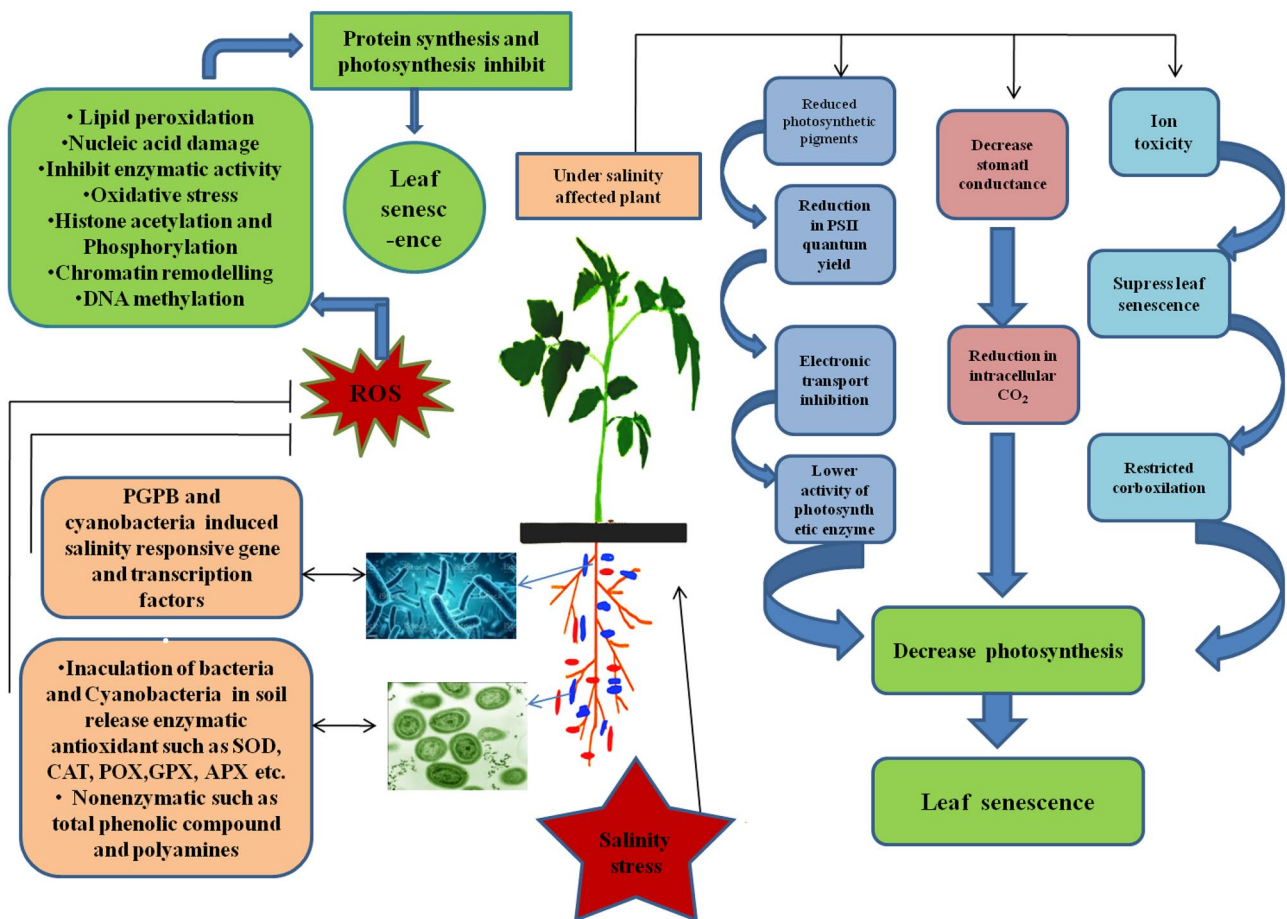


Fig. 2 Mechanism of inducing salt tolerance by microbial community in plant

exchanged Trp and thiamine as a cross-species communication for IAA produced by *A. brasilense* [68]. Sulfobacteria interaction with diatom (*P. multiseriens*) is also another such example in which the conversion of Trp, released by diatoms, into IAA. Furthermore, synthesized IAA can act as the signaling molecule to encourage diatom cell development. A positive feedback loop exists when cross-kingdom signaling occurs in this way. Under diverse environmental stress, IAA notably enhanced the development of a mutualistic connection between multiple organism systems in the environment [117]. Stress-responsive genes controlled by PGPR may have an impact on plants that display induced systemic tolerance. *Arabidopsis* expresses many genes including BAB18 (which codes for LEA proteins) and ERD15 (which codes for the early response to dehydration) in response to *P. poly-myxa* inoculation [31].

PGPB either directly affects plants by synthesizing phytohormones or indirectly by stimulating signaling in the host. Hence, the interaction of salt-tolerance microbes with their host on the gene level has been proven to be effective in alleviating salt stress resistance. For example, tomato (*L. esculentum*) expressed the *codA* gene of *A. globiformis*, which encodes choline oxidase. It stimulated the production of glycine betaine and increased the plant's salt tolerance [12]. Another study revealed that *D. natronolimnaea* STR inoculation affected the transcriptional machinery essential for salinity tolerance in wheat plants by controlling genes related to the SOS pathway (gene SOS1 and SOS4) [10]. Furthermore, increased gene expression of antioxidant enzymes such as ascorbate peroxidase (APX), catalase (CAT), and superoxide dismutase (SOD), as well as higher proline content, were also reported in PGPR-inoculated wheat plants [94]. As a result, the use of beneficial stress-tolerant microorganisms not only improves the microbial composition but also improves ecological compositions. The

two cyanobacterial species, *N. entophytum* and *O. angustissima* have also been used as biofertilizers for pea plants in place of the usual chemical fertilizer in salinity. Under salt stress conditions, *M. aeruginosa* and *P. agardhii* can produce cyanopeptides such as microcystins and anabaenopeptins. These compounds may affect plant physiology by modulating intracellular processes like osmotic adjustment, antioxidant defense, hormonal balance, gene expression, and metabolite synthesis [25, 29, 65].

To detect and react to environmental challenges, some eukaryotes, plants, yeast, and bacteria use two-component systems, which are sensor-responsive circuits. RppA (Regulator of photosynthesis and photopigment-related gene expression A) or Rep1 (Response regulator 1) is a response regulator protein that was studied as part of a two-part system that included a sensor histidine kinase (Hik2). These Hik2 are released by cyanobacteria. The various methods by which bacteria and cyanobacteria participate in cell signaling pathways under salinity are summarized in Table 1.

- Signaling via ROS: ROS are highly reactive chemicals that can oxidatively harm biological components. However, ROS also function as signaling molecules that control several cellular functions, including ion transport, gene expression, and enzyme activity [86]. Salt stress causes an increase in ROS production, which in turn activates stress-responsive genes and antioxidant enzymes. To modulate salt tolerance, ROS also interacts with other signaling molecules such as Ca^{2+} , NO, H_2S , and phytohormones [103]. Antioxidants produced by bacteria and cyanobacteria can scavenge ROS and shield plant cells from oxidative damage. For instance, glutathione peroxidase (GPX) and superoxide dismutase (SOD), which lower ROS levels in plants, can be produced by cyanobacteria [26]. *Enterobacter cloacae* regulate the

Table 1 Control of plant gene by the microbial cell signaling molecule released in salinity stress

Gene expression	plant	Microorganism	Mode of action	References
Constitutive triple response1 (CTR1)	Wheat	<i>Arthrobacter protophormiae</i> (SA3) and <i>Dietzia natronolimnaea</i> (STR1)	(ABA)/ACC content, and regulate the expression of a regulatory component (CTR1) of the ethylene signaling pathway	[8]
TaMYB and TaWRKY	Wheat	<i>Dietzia natronolimnaea</i> STR1	Regulates the expression of stress-responsive genes, involving induction of TaMYB and TaWRKY expression	[10]
DREB2b, RD29A, RD29B, and RAB18	<i>Arabidopsis</i>	<i>Enterobacter</i> spp.	Increases IAA production, induces expression of salt stress-responsive genes	[39]
TF bZIP24	<i>Arabidopsis</i> (in salt sensitive species)		Regulate stress adaptive pathways	[28]
rbcL and WRKY1	<i>Arabidopsis thaliana</i>	<i>Klebsiella</i> sp.	Modulates rbcL and WRKY1 genes expression	[84]

salinity stress response antioxidant enzyme in maize plant. In another study, *P. boryanum* and *O. acuta* has been shown to regulate ROS in rice leaf through the production of antioxidant enzyme peroxidase under salinity stress [114]. *P. Pseudomonas* enhanced agricultural outcomes through the production of proline and antioxidant enzymes in the root system and shoots of plant [17].

- **Ca²⁺ signaling:** In plants, Ca²⁺ acts as a universal secondary messenger to transmit a variety of signals. Its levels are controlled by channels, pumps, and transporters present in the plasma membrane and endomembrane system. Under conditions of salt stress, salt sensors or ROS production cause Ca²⁺ efflux, this sets off a series of processes involving Ca²⁺ binding proteins such as calmodulin and calcineurin B-related proteins. These proteins influence gene expression and cellular responses by interacting with downstream targets such as protein kinases and transcription factors [2, 32]. By generating Ca²⁺ binding chemicals or changing Ca²⁺ transporters, bacteria and cyanobacteria can modify Ca²⁺ signaling in plants [6]. For instance, bacteria can synthesize EPS that binds Ca²⁺ ions and controls how readily available they are to plant cells. In a study, *Bacillus aryabhatai* increased *Solanum lycopersicum* potential to endure salt by producing exo-polysaccharides [116].
- **Signaling through phytohormones:** The organic substances that control the growth and development of plants are known as phytohormones. Stress responses also involve several phytohormones, including ethylene, salicylic acid, jasmonic acid, and abscisic acid (ABA) [107]. ABA is produced when plants are under salt stress, and it builds up in plant tissues. A signaling network that includes protein kinases, phosphatases, transcription factors, and ion channels is activated when ABA binds to its receptors [45]. Stomatal closure, osmotic control, gene expression, and adaptive growth are all regulated by ABA signaling. Interacting with ABA signaling or other metabolic pathways eg: ethylene, SA, and JA also affect salt tolerance [103].

Phytohormones can be synthesized, or its biosynthesis can be controlled by bacteria and cyanobacteria in plants in harsh environment. Phytohormones-ABA synthesized in salinity stress through which plant can improve tolerance in such condition. Phytohormone are also used as plant growth regulator, they can control plant morphology such as plant height, enhance branching, promote flowering, and regulate fruit development. Bacteria, for instance, can produce IAA or ACC-deaminase, which impacts the amounts of auxin or ethylene in plants. Under salt stress, cyanobacteria can synthesize cytokinin that promote plant growth [6]. Under salinity stress circumstances, endophytes, and plant

growth-promoting bacteria (PGPB) also have a substantial impact on the induction of plant signaling. Under salt stress in *T. aestivum*, *A. protophormiae* (SA3) and *Dietzia natronolimnaea* (STR1) alter the expression of the DREB2 transcription factor and the ethylene signaling regulatory compartment (CTR1) pathway as well as increasing IAA and reducing ABA and ACC levels [8]. There are various cyanobacterial species are involved in reducing salt stress in different plant species are listed in Table 2.

Importance of Microbial Exopolysaccharide in Maintaining the Osmotic

EPS is a crucial factor since it enables crops to flourish in challenging environments. EPS consists of biopolymers such as polyester, polyamides, and polysaccharides [79]. Polysaccharides stimulate macropore development and increase soil particle adhesion, which enhances soil porosity and aeration. Soil microorganisms can improve plant nutrient uptake and raise the water potential of the soil by generating EPS around the roots [42]. The slime structure of the EPS helps to bind the soil through multiple bonding such as H-bond, cation-anion interactions etc. which helps to improve bacteria and cyanobacteria's capacity to hold water and regulate the diffusion of organic carbon sources. As a result, a slimy substance develops around the soil aggregates, protecting them from salinity and dryness. Plants that have been modified with EPS-producing bacteria exhibit resilience to salinity and water shortage [104]. Exopolysaccharides and extracellular proteins are just a couple of the polymeric compounds that some cyanobacteria can make outside of their cells [78]. Such a phenomenon has been reported by [19] where the inoculation with *P. putida* strain GAP-P45 in saline soil increased the aggregate stability of the soil [19]. The EPS production can be done on a large scale by using multiple organisms such as *Pseudomonas*, *Bacillus* and *Paenibacillus*. Additionally, after simulating rainfall, strains of *Streptomyces* and *Penicillium* significantly reduced soil erosion and loss by releasing exopolysaccharide which promotes the aggregation of soil particles.

Various genera of microbial taxa synthesize a variety of EPS which differ significantly in their composition and behavior [11, 20]. Multiple monosaccharides such as mannose, glucose, xylose etc. can be found as the monomeric subunit of these EPSs [113]. Glucose is the primary monosaccharide component of the EPS produced by *Mesorhizobium sp. Semia* 816, followed by galactose and mannose [81]. The monosaccharides, disaccharides and polysaccharides released by these microorganisms work as the carbon sources for another microbial component of the soil biosphere. Hence releasing saccharides, peptides, and enzymes extracellularly promotes the fixation of nitrogen and plant growth promotion, due to the salinity [15]. Some examples

Table 2 Various microbial extracellular compounds release in high salinity and their role in enhancing the salt tolerance in plants

Cyanobacterial strain	Plant	Mechanisms	References
<i>Anabaena vaginicola</i> ISB42, <i>Nostoc calcicola</i> ISB43, <i>Trichormus ellipsosporus</i> ISB44, and <i>Cylindrospermum michailovskoense</i> ISB45	<i>Mentha piperita</i>	Growth promotion in plant	[1]
<i>Lyngbya mucicola</i> ; <i>Oscillatoria Princeps</i> L.; <i>Lyngbya phormidium</i> <i>Gloeocapsa</i> sp.; <i>Cryophilic</i> sp.	<i>Oryza sativa</i>	Increase in soil organic matter and increase in plant nutrient content	[34]
<i>Nostoc carneum</i> TUBT04 and <i>N. carneum</i> TUBT05	<i>Oryza sativa</i>	Plant growth and yield improvement	[16]
<i>Nostoc flagelliforme</i>	<i>Arabidopsis thaliana</i>	P-loop-based transformation in plants gene for NTPase domain	[21]
<i>Anabaena doliolum</i> , <i>Phormidium fragile</i> , <i>Anabaena oryzae</i> , <i>Calothrix geitonos</i> , <i>Hapalosiphon intricatus</i> , <i>Aulosira fertilissima</i> , <i>Tolypothrix tenuis</i> , <i>Oscillatoria Acuta</i> , and <i>Plectonema boryanum</i>	<i>Oryza sativa</i>	Promotion of growth and control of phytohormone concentration	[62]
<i>Scytonema hofmanni</i>	<i>Oryza sativa</i>	Production of a hormone similar to gibberellins	[80]
<i>Nostoc kihlmani</i> and <i>Anabaena cylindrica</i>	<i>Triticum aestivum</i>	Better soil structure and increased growth	[27]
<i>Anabaena sphaerica</i>	<i>Oryza sativa</i>	Production of extracellular proteins and polysaccharides	[54]
<i>Nostoc muscorum</i> ; <i>Anabaena fertilissima</i> , <i>A. anomala</i>	<i>Oryza sativa</i>	Rising rhizosphere biology or phytohormone levels	[1]
<i>Anabaena variabilis</i>	<i>Medicago truncatula</i>	plants that have the flavodoxin gene transform	[18]
<i>Plectonema boryanum</i> and <i>Oscillatoria acuta</i>	Rice (leaf)	Enzymatic activity of phenylalanine ammonia-lyase and Peroxidase increases	[114]
Bacterial strain			
<i>Pseudomonas</i> sp	<i>Arabidopsis thaliana</i> - <i>Gossypium hirsutum</i>	Germination rate increases	[17]
<i>Trichoderma</i> sp.	<i>Brassica napus</i>	Increase tolerance to salinity and seed biomass	[24]
<i>Bacillus species</i>	<i>Solanum lycopersicum</i>	Increase the production of proline, the activity of antioxidant enzymes, the amount of chlorophyll and carotenes, and the prevention of cell membrane damage	Yoo et al.,2019
<i>Bacillus species</i>	<i>Capsicum annum</i>	Better growth and development, Increased levels of carotenoid and chlorophyll, Increased levels of salicylic acid, both under and during stressful conditions Under stress, secrete IAA, ACC, and more proline	[37]
<i>Azotobacter vinelandii</i> (SRIAz3)	Wheat (<i>Triticum Aestivum</i>)	Higher levels of proline, IAA, zeatin, gibberellins, and malondialdehyde	[83]
<i>Pseudomonas</i>	Cotton (<i>Gossypium Hirsutum</i>)	Salinity tolerance through IAA phytohormone regulation	[23]
<i>Bacillus pumilus</i> strain FAB10	Wheat (<i>Triticum Aestivum</i>)	Root surface biofilm development, increased EPS, IAA, ACC deaminase activity, and solubilized phosphate	[5]
<i>Pantoea</i> sp. and <i>Enterococcus</i>	Mung bean (<i>Vigna radiata</i>)	Increased plant growth and ACC deaminase activity result in an increase in salt tolerance	[72]
<i>Pseudomonas syringae</i> ; <i>Pseudomonas fluorescens</i> ; <i>Pseudomonas fluorescens</i> and <i>Rhizobium phaseoli</i>	Mung bean (<i>Vigna radiata</i>)	Under salinity stress conditions, contain ACC deaminase, lower ethylene synthesis, and increase nodulation	[3]
<i>Arthrobacter protophormiae</i>	Pea (<i>Pisum sativum</i>)	Increases ACC deaminase activity, bacterial diversity colonization, and salinity stress defence	[7]
<i>Hartmannibacter diazotrophicus</i>	Barley (<i>Hordeum Vulgare</i>)	Reduce salt stress by activating ACC deaminase	[100]
<i>Burkholderia</i> sp. MTCC 12259	Wheat (<i>Triticum Aestivum</i>)	Increase production of ACC deaminase	[85]
<i>Serratia</i> sp. SL- 12	Wheat (<i>Triticum Aestivum</i>)	Under salinity stress, ACC deaminase and plant growth promotion	[94]

Table 2 (continued)

Cyanobacterial strain	Plant	Mechanisms	References
<i>Streptomyces sp.</i>	Tomato (<i>Solanum Lycopersicum</i>)	Proline and ACC deaminase production as well as plant growth promotion	[69]
<i>Bacillus</i>	Peppers (<i>Capsicum Annuum</i>)	Plant ethylene production is decreased and salinity stress tolerance is promoted by ACC deaminase activity	[112]
<i>Hartmannibacter diazotrophicus E19</i>	<i>Arabidopsis thaliana</i>	EPS and ACC deaminase Production	[100]

of EPS produced by various cyanobacteria under salinity stress are listed in Table 2. Fertilizers are a common source of salts applied to soil, and their excess can have a significant effect on soil salinization. Out of all the mineral fertilizers, potassium chloride has the greatest effect on soil salinity because plants can readily absorb potassium as a macronutrient whereas chloride, a micronutrient, remains in the soil. High concentrations of chloride ions may be detrimental to plant growth and yield, much like Na^+ ion. For example, Cl^- inhibits photosystem II's effectiveness, disrupting photosynthesis, and interacts with other essential plant growth anions such as PO_4^{2-} and NO_3^- [49]. It has been demonstrated that introducing various bacterial strains into plants causes an increase in plant growth and a decrease in Cl^- uptake. Reduction in Cl^- ion in faba beans inoculated with a melatonin and EPS-producing *Azotobacter chroococcum* strain. However, because carboxyl and hydroxyl functional groups predominate in bacterial EPS, most of these EPS are negatively charged, suggesting that the drop-in chloride anion concentration in bacteria-inoculated plants may not be due to the EPS's ability to adsorb Cl^- [58]. Subsequently, these activities of the micro-engineers develop a surrounding that nullifies the effects of salinity.

The addition of these EPS-producing microbes can have a very impactful effect on plant productivity under salt stress. One of the studies used the potential of *Planococcus rifietoensis RT4* and *Halomonas variabilis HT1* in chickpeas and observed a many-fold improvement in the characteristics under the high salinity [75]. In saline environments, EPS may control the microsphere composition and can limit sodium (Na^+) uptake by plants. Additionally, EPS plays a significant role in the development of relationships between plants and microbes [78]. It has been observed that *Bacillus drentensis* and *Enterobacter cloacae* can improve salt tolerance by enhancing nutrient and water uptake by forming biofilm in the root zone of mung beans [79]. By lowering the Na^+ level that is accessible for plant uptake, EPS mitigates the negative consequences of salt stress. Microbes like *Pseudomonas PS01* can use their EPS to regulate the lipoxygenase (LOX2) gene which plays a significant role in the jasmonic acid (JA) synthesis pathway. JA-pathway is the main component of the plants against multiple abiotic stresses [9]. Similarly, *Pseudomonas anguilliseptica SAW24* is involved in enhancing the plant height and biomass of

Faba beans under high salinity [9] while *Aeromonas spp.* SAL-17 and SAL-21 increase the salt tolerance in wheat plants by improving multiple physiological parameters such as proline content, nitrate reductase activity, transpiration rate, and root shoot length [59]. Cyanobacteria, specifically the species *Nostoc spp.* and *Anabaena spp.*, have special qualities of binding sodium ions and forming biofilms that make them useful for remediating salt-affected soils [79].

Role of microbial-based Volatile Organic Compounds (VOCs) in Promoting Salt Tolerance in Plant

VOCs are low molecular weight, lipophilic compounds that have low boiling points and high vapor pressure. They are mainly synthesized by the microbes and have multi-dimensional functions. Indirect interactions between plants and microbes are made possible by these compounds, which enable function as short- and long-distant signals dissemination in the rhizosphere [52]. They are tiny molecules from many chemical classes that easily diffuse and evaporate through holes filled with air and water. VOCs are the perfect signal candidates in interactions with plant roots because of these characteristics [46]. It was discovered that bacteria produce over 1000 VOCs and non-organic volatile chemicals, some of which improve agricultural plant quality and yield [105]. The bacterial VOCs control the physiology and hormonal balance in the plant. It can also influence photosynthesis abilities, defense mechanisms, and nutrient uptake under harsh conditions [101]. In *Arabidopsis*, VOCs produced by *B. subtilis GB03* activate a variety of hormonal signals, including auxin, cytokinins, brassinosteroids, gibberellins, and salicylic acid. *Paraburkholderia phytofirmans* produced 2-undecanone, and 3-methylbutanol, which improved plant development and resistance to salinity stress. [44, 82]. The control of the Na^+ flux is the primary mechanism by which bacterial VOCs develop systemic tolerance in plants to saline conditions. These mechanisms are majorly governed by the transport proteins, including *HKT1* and *SOS1* [64]. Bacterial VOC promotes the expression of the *HKT1* gene, which in turn speeds up the removal of sodium ions from xylem sap and plant leaves. This phenomenon has been explored by Panpatte et al. [71] and Cappellari et al. [14] where the higher biomass yield and lower sodium content are observed

after the treatment with the GB03 VOC in *Arabidopsis* plants. The SOS3 (salt overly sensitive 3) calcium-signaling sensor may also help with salinity tolerance that is mediated by VOCs of plant growth-promoting bacteria [71]. Volatile compound-induced salt tolerance by *Pseudomonas simiae* strain AU was seen in soybean plants where VOCs not only reduced root Na^+ levels but also boosted proline accumulation, which protects cells from osmotic stress. Additionally, the hiked levels of vegetative storage protein (VSP) along with other essential biomolecules have been observed in AU-treated plants [71]. Multi-types of biomolecules such as alcohols, Alkanes, Ketones etc. can be part of the VOCs released by *Chlamydomonas reinhardtii*. Due to an increase in reactive oxygen species (ROS) during salt stress, *Solieria chordalis* and *Gymnogongrus antarcticus* produced more halogenated hydrocarbons. VOCs can also function as an inhibitor to promote the survivability of plants under stress [64].

Role of Microbial Secondary Metabolites in Salinity Stress

Microbial release of secondary metabolites such as cytokinin, gibberellins, and indole acetic acid (IAA) have a very potent role in tackling salinity stress. A crucial physiological signal called ABA controls the expression of numerous genes that respond to osmotic and salt stress. These genes are responsible for controlling the water flux around the plant which is most hit under high salinity. Abiotic stressors in plants also cause them to respond with salicylic acid (SA) and brassinosteroids (BR) [37]. Under salt stress, rice seedlings produced more endogenous SA and showed an increase in the activity of SA biosynthetic enzymes. Plants can tolerate salt better in the presence of the exogenous application of SA and BR [115]. In barley, SA increased the amounts of carotenoids and chlorophyll and preserved membrane integrity in saline circumstances. BR promotes the activities of superoxide dismutase (SOD), Peroxidase (POX) and APX and enhances the production of tocopherol, ascorbate, and reduced glutathione. *Synechococcus* 6301 under salt stress increased cytochrome oxidase and HC/NaC antiport activities. IAA levels in *Nostoc carneum* TUBT04 and *Nostoc carneum* TUBT05 were increased in salinity [16]. Additionally, it was found that neither of the cyanobacterial strains required tryptophan as a precursor for IAA production. Gibberellins and cytokinins were also found in *Anabaena cylindrica* and *Nostoc commune*. *Actinobacteria*, *Nocardia*, *Frankia*, *Kitasatospora*, and *Streptomyces* are some of the bacteria that produce IAA. Abscisic acid (ABA), often known as the stress hormone is increased in the root zone when there is a water shortage due to salinity stress [42]. Under salinity, the amount of ABA rises, which aids the plant in reducing the effects of stress. In root

vacuoles under salinity, ABA aids in the accumulation of compatible solutes such as proline and carbohydrates. It demonstrates that *Bacillus subtilis* GB03 and *Pseudomonas putida* R-168 enhanced the surface area of thicker roots and root dry weight in Maize seedlings under salt stress [49, 70, 97]. Bacteria can also produce gibberellins, which aid in promoting plant growth and productivity. According to [61], the overproduction of proline, ABA, trans-zeatin riboside, GA3, and IAA led to an increase in root and shoot length and biomass when a halo-tolerant bacterium was introduced into soybean plants. While certain PGPRs are proven to metabolize ABA and have varying effects when exposed to salinity stress, other PGPRs are demonstrated to aid in its synthesis [74]. Various secondary metabolites synthesized by microbes under salt stress are listed in Table 2.

Role of Microbial-based Osmo-Protectants in Salt Tolerance in Plants

Microorganism synthesizes organic osmolytes in the cytoplasm to maintain their osmotic condition and to enhance plants' reactions to such stress. In addition, osmoprotectants like proline, betaine, trehalose, glycine, phenols, and flavonoids were produced by helpful bacteria like *Azospirillum*, *Burkholderia*, *Arthrobacter*, *Bacillus*, *Pseudomonas*, and *Rhizobium* [108]. Additionally, osmoprotectants made by bacteria are biosynthesized quicker than those made by plants that relate to them. Heterotrophic bacteria like *Pseudomonas* and *Stenotrophomonas* strains, as well as cyanobacteria with moderate salt tolerance like *Synechocystis* sp. PCC 6803 and *Synechococcus* sp. PCC 7002, can de novo synthesize and store glucosylglycerol (GG) as an osmo-protectant. GG can be used to stabilize the proteins and enzymes such as superoxide dismutase in plants [42, 92]. According to the extensive knowledge gained through genome mining, halotolerant cyanobacteria have extended gene families and/or clusters that code for enzymes that produce specific osmoprotectants such glycine betaine (GB), betaine derivatives, and mycosporine-like amino acids (MAAs), among others [108].

Release of Microbial-based Antioxidants in Salt Stress and their Role in Salt Tolerance in Plants

In *Synechocystis* and *Anabaena*, different antioxidative mechanisms have been stimulated in response to increased saline content [82]. Under harsh conditions, multiple ROS are produced in the plant cell. ROS can damage cell integrity and significantly oxidize substances [103]. The antioxidant enzymes such as SOD, CA, GPX etc. are key machinery that tackles the ROS in the plant system. The synthesis of these enzymes can be controlled by symbionts like *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* [98]. In

tomato plants which are exposed to high salt concentrations, increased SOD, CA, APX, GR, and GST activities were found which are controlled by *Sphingomonas sp.*, *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* [42].

Even though ascorbate is one of the important antioxidants in plant cells, applying it exogenously helps plants recover from stress and reduces the negative effects of salt. Additionally, the effects of salt stress on plants are lessened by the exogenous administration of glutathione as a free radical scavenger. Other nonenzymatic antioxidants that are able to protect plants from oxidative stress include the vitamins C and E, carotenoids, and lipoic acid [82].

Conclusion

Salinity stress, in plants can have negative effects on society and the economy along with the environment. Plant growth and yields can be heavily damaged as a result of the changing environmental circumstances. Plant cells synthesize ROS as salinity stressors increase, which reduces ecological fitness. In the ensuing decades, the situation will worsen, endangering plant life. Plants enlist antioxidants to maintain a balance between the production and quenching of ROS. Through several mechanisms, PGPB can play a significant role in mitigating abiotic stress in their host. It can control many pathways such as the antioxidant system, osmotic adjustment, and metabolic reprogramming by releasing multiple extracellular compounds such as phosphate solubilization, nutrient mobilization, phytohormone and VOCs. Therefore, PGPB and cyanobacteria are excellent alternatives to conventional fertilizers because of their affordability, environmental friendliness, and sustainability to boost plant tolerance to a variety of conditions, such as salinity and drought.

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Declarations

Conflict of interest There is no conflict of interest for this manuscript. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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