NATURE & SCIENCE
October 2026, Volume 8, Issue 5, pp. 40–60
DOI: https://doi.org/10.36719/2707-1146/68/40-60

Current Understanding of PGPR–Plant Interaction under Salt Stress Environment: A Review

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Abstract. *Soil salinity is a serious environmental problem which affects agricultural production globally, especially in arid and semi-arid areas. Soluble salt accumulation may affect water uptake, induce ionic toxicity, decrease nutrient availability and increase reactive oxygen species (ROS) production that leads to damage to cellular components and affects normal physiological functioning. Traditional breeding has developed salt-tolerant crops, but long breeding cycles, high costs, and genotype–environment interactions limit its efficiency. Plant growth-promoting bacteria (PGPB) offer an eco-friendly alternative for improving crop performance under salinity. They enhance salt tolerance through complementary mechanisms, including phytohormone regulation, osmolyte accumulation, exopolysaccharide production, nutrient acquisition, and balanced Na^+/K^+ uptake. PGPB also promote proline and glycine betaine accumulation, supporting osmotic adjustment, membrane stability, and cellular protection. Together, these microbial activities help plants maintain ionic and physiological balance, reduce salt-induced damage, and sustain growth under saline conditions. This review brings together the physiological responses of the crop plants to salinity and discusses both the direct and indirect mechanisms mediating salt tolerance that PGPB provide based on fundamental and contemporary (2020–2026) literature. Representative plant-bacterium associations are curated in comparative tables to showcase the taxonomic diversity and mechanisms already described, and existing knowledge gaps are highlighted, including at the field-level and in the context of multi-strain consortia. The use of PGPB is proposed as a low-cost, non-toxic, and eco-friendly solution to maintain crop productivity in salinity affected soils, and to help ensure long-term food security in the face of climatic changes.*

Keywords: *soil salinity, plant growth-promoting bacteria, reactive oxygen species, sustainable agriculture, food security*

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Received: 4 June 2026; Accepted: 10 September 2026; Published online: 25 October 2026
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1. Introduction

Climate change is among the most pressing environmental issues in the 21st century. However, a large amount of evidence exists that intensive agriculture and increased energy usage are significant anthropogenic drivers of global climatic changes that include higher temperatures, variability in rainfall, flooding and degradation of soils (Ansari et al., 2021; Kopittke et al., 2026). Soil salinisation is one of these consequences and is especially problematic in areas with limited water resources, such as in arid and semi-arid regions, where it further impacts agricultural sustainability (Janni et al., 2024; Shokri et al., 2024).

Salinity in soils occurs when soluble salts slowly build up in the soil profile to levels that inhibit plant growth and soil activity. There are two types of salinisation; the first is through geological and climatic processes (primary) and the second is due to human activities such as inappropriate irrigation practices, inadequate drainage, and unsuitable land-use (secondary) (Stavi et al., 2021; Hassani et al., 2021). The high concentration of soluble salts is the most typical characteristic of saline soils and can be used to determine salinity status of soil, typically by measuring the electrical conductivity of the saturated soil extract at 25 °C, with a value above 4 dS m^{-1} indicating saline soils (Liu et al., 2026).

While NaCl is generally regarded as the main salt causing salinity stress it can be other salts such as sodium sulfate that "can play a significant role in salinity" related issues. Ions like sodium (Na+), calcium (Ca2+), magnesium (Mg2+) and carbonate species can build up in the soil over time, causing fertility problems and impacting plant growth (Negacz et al., 2022). Now, it is known that salinity is one of the most significant causes of land degradation worldwide, with over 833 million hectares of agricultural land already impacted by salt and the number of such affected areas anticipated to grow with the ongoing climate change and unsustainable land management practices (Liu et al., 2026; Alhan et al., 2026).

The development and severity of soil salinity are influenced by several factors related to the environment and anthropogenic such as climate, water irrigation quality, soil properties, hydrology, topography, biological activity, and land use practice (Basak et al., 2022). Beyond soil degradation, crop productivity and economic return in saline environments has been found to be lower, with losses reported across a range of staple crops including rice, wheat, cotton and sugarcane – particularly in agricultural areas such as India (Kopittke et al., 2026; Derbew et al., 2026).

When plants encounter saline conditions, they use various adaptations to cope with the stress, typically either by avoiding the stress (to minimise the damage) or tolerating the stress (to keep growing and living normally despite the stress). Under conditions where salinity levels are high enough, however, plant growth and yields can be significantly reduced, to a higher or lower degree depending on the species and cultivars (van Zelm et al., 2020; Liu et al., 2024).

Salinity effects are of a multifaceted nature in terms of physiology and biochemistry. "A high salt concentration decreases the soil water potential to which plants" must adjust, making it harder for them to absorb water, and causing osmotic stress. With limited water supply, the shoots keep growing less and more, and the stomata begin to close, which decreases the transpiration rate and the efficiency of photosynthesis (Hasanuzzaman et al., 2023). As salinity continues, toxic ions, especially sodium and chloride are increasing in plant tissues, which alters the organisation, integrity and metabolism of cells (Tester & Davenport, 2003).

Salinity also affects uptake and uptake of mineral nutrients. The antagonistic effects of toxic ions and nutrient elements may cause deficiency of N, P, K, Ca, Mg, Fe, Cu, Zn and other plant growth elements (Dey et al., 2021). High accumulation of salt further disrupts the photosynthetic apparatus, elevates the overproduction of Reactive Oxygen Species (ROS) causing oxidative stress and

programmed cell death (PCD) in proteins, lipids, nucleic acids and cellular membranes (Hasanuzzaman et al., 2021). Salinity hence negatively impacts the plant growth from the germination to the vegetative growth stage, flowering and reproduction stage (Manono, 2025).

As saline soils are becoming more common, sustainable strategies to enhance soil productivity in saline environments have become more relevant (Xing et al., 2026). Salinity mitigation through conventional management strategies, including irrigation, drainage enhancement, soil amendment and the development of salt-tolerant cultivars, has helped reduce salinity, but can be expensive, labour intensive, location-specific and will not provide a long-term solution (Melino & Tester, 2023). To devise more effective management strategies, a better understanding of the molecular, physiological and ecological mechanisms of plant response to salinity is needed (Singh, 2022).

In the last few years, plant growth-promoting bacteria (PGPB) have gained a lot of attention in recent years as environment-friendly bioinoculants that are able to increase the resistance of plants to saline conditions (Mishra et al., 2021). They promote plant growth and productivity in a diverse range of ways such as nutrient uptake, ion homeostasis, control of phytohormone levels, water relations, antioxidant defence, and stress responsive pathways (Ilangumaran & Smith, 2017; Shahid et al., 2026). Owing to these multifaceted benefits, PGPB are increasingly considered a promising biological tool for sustainable crop production in salt-affected environments, and PGPR-based bioinoculants are also being explored in combination with mycorrhizal fungi and engineered soil microbiomes to further extend crop resilience under climate-driven salinity (Shi et al., 2026; Chanson et al., 2026; Zeng et al., 2024).

Accordingly, “this review aims to provide a comprehensive, critically referenced overview of the mechanisms through which plant growth-promoting bacteria alleviate salinity stress and enhance plant performance under saline conditions”. The review brings together literature on both the basics of stress tolerance mechanisms exerted by PGPB and more recent advances in the same field (de Andrade et al., 2023; Chakrovarty et al., 2026; Nguyen et al., 2025) and points to the potential of using these microbes in sustainable agriculture under the new challenges of increasing salinity.

2. The Plant's Response to Salinity Stress will be Physiological

As dissolved ion concentration increases in soil, soil becomes saline and can become saline, sodic or saline-sodic soil. Salinity-affected soils typically have elevated concentrations “of cations like Ca^{2+}, Mg^{2+} and Na^{+}, and anions like SO_4^{2-}, Cl^{-} and HCO_3^{-}”. Of these, the sodium and chloride ions are clearly damaging because of their toxicity to plant physiology and their ability to cause disruption of soil structure (Tester & Davenport, 2003; Ansari et al., 2024).

Plants are impacted by salinity at the morphological, physiological and biochemical level. It can inhibit seed germination, inhibit vegetative growth and affect reproductive development by osmotic stress, causing roots to have trouble absorbing water, and ionic stress, from the accumulation of toxic ions in the plant tissue. These stresses over time lead to soil erosion, reduced soil fertility and reduced yields. In addition to these primary effects, salinity also generates secondary effects, known as oxidative stress, whereby an excess of ROS damages cellular membranes, proteins and DNA. These all together effects are harmful for the growth of the plants and endanger the sustainability of agriculture in salt affected areas (Liu et al., 2026).

2.1. Disruption of Water Uptake

2.1.1. Osmotic Stress

“Osmotic stress is one of the first responses of plants to salinity. Too much salt in the soil solution decreases its water potential, decreasing the water potential gradient and making it harder for water

to enter roots". Under these conditions, plants also have a water deficit despite the presence of adequate soil water and adjust by reducing the openings of their stomata and minimising transpiration, a process that is known to help conserve water but also reduces their ability to fix carbon dioxide (CO2) (Tester & Davenport, 2003).

2.1.2. Cellular Dehydration

When the osmotic stress is continuous, the turgor pressure of the cell decreases, which will prevent it from growing. Loss of turgor manifests as leaf wilting, reduced leaf-area development, and inhibited elongation of shoots and roots. Prolonged dehydration reduces meristematic activity, which in turn slows the production of new tissues.

2.2. Rhizobacteria-Derived Biomolecules Contributing to Plant Tolerance and Resistance

2.2.1. Production of Plant Growth-Regulating Compounds

Saline "conditions cause plants to" synthesise several phytohormones, including abscisic acid "(ABA), indole-3-acetic acid (IAA), and ethylene, which regulate plant" metabolism, morphology, biomass accumulation, and physiological adjustment. Soil microorganisms can additionally modify the plant's hormonal status by releasing phytohormones or hormone-modulating enzymes of their own. "Modifications in hormonal signalling arising from plant-microbe interactions are consequently regarded as a significant mechanism contributing to plant tolerance of soil salinity" (Ilangumaran & Smith, 2017).

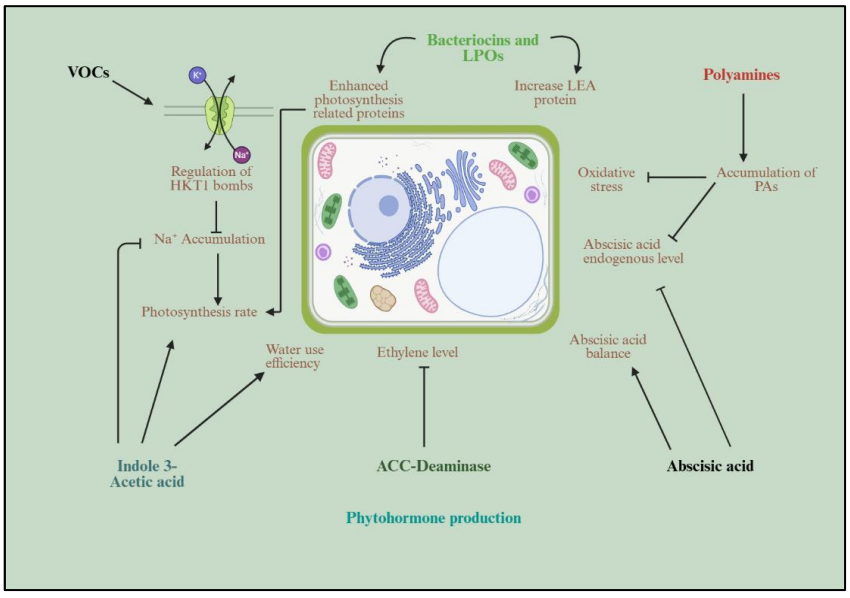


Figure 1

Molecules synthesized by plant growth-promoting bacteria (PGPB) implicated in plant salinity tolerance, including indole-3-acetic acid, ACC deaminase, abscisic acid, volatile organic compounds, polyamines, and bacteriocins/lipo-chito-oligosaccharides, and their downstream physiological effects.

Source. Original figure prepared by the authors, synthesised from the mechanistic evidence discussed in Section 2.2 (Ilangumaran & Smith, 2017, and the primary studies cited there in).

2.2.1.1. Indole-3-Acetic Acid (IAA)

Indole-3-acetic acid (IAA) is the key auxin governing plant growth and development. IAA is synthesised by rhizobacteria through several metabolic routes, many of which depend on L-tryptophan supplied by root exudates. This hormone regulates a range of plant "processes, including

cell division, cell elongation, tissue differentiation, apical dominance, phototropism, and gravitropism"; a balanced IAA concentration supports normal growth, whereas excessive levels can be inhibitory.

External "application of IAA to crops such as maize, sorghum, and pea has been shown to reduce the adverse effects of salinity stress, improving photosynthetic activity, water-use efficiency", regulation of sodium ion accumulation, and biomass. Increased auxin levels under saline conditions are considered important for supporting root and shoot growth, which are particularly sensitive to this abiotic stress.

Auxin-producing PGPB also limit the yield losses typically caused by soil salinity. Inoculation of salt-stressed cotton with the IAA/ABA-modulating strain *Pseudomonas putida Rs-198* improved germination, productivity traits, and nutrient content while lowering internal ABA synthesis (Yao et al., 2010). Comparable benefits have been reported in groundnut inoculated with halotolerant IAA-producing rhizobacteria under 100 mM NaCl, which enhanced water-status maintenance and productivity traits (Shukla et al., 2012; Ansari et al. 2019). In wheat, inoculation with the "auxin- and siderophore-producing *actinobacterium Streptomyces sp.* under saline soil conditions" increased germination rate, seedling length, biomass, and nutrient content (Sadeghi et al., 2012), while in common bean, IAA-producing *Azospirillum brasilense* and *Rhizobium etli* increased root biomass, root number, and nodulation relative to IAA-deficient mutants, directly implicating bacterial auxin in the root-developmental response (Remans et al., 2008; Ansari et al., 2023).

These findings collectively support a strong relationship between bacterial IAA production and modification of plant hormonal balance in a manner that promotes growth under saline conditions. Comparisons between externally applied IAA and auxin-deficient bacterial mutants indicate that bacterially derived auxin differentially affects root biomass, nodule formation, and basal root development during early growth stages (Ilangumaran & Smith, 2017).

2.2.1.2. Ethylene Regulation Through ACC Deaminase Activity

Ethylene is widely recognised as a stress-related hormone, and its synthesis is strongly affected by both abiotic and biotic stress. Increased ethylene levels reduce root elongation and formation and therefore have an overall negative effect on plant growth. The immediate precursor of ethylene biosynthesis, 1-aminocyclopropane-1-carboxylate (ACC), is transported to stress-affected tissue, where it is oxidised to ethylene by ACC oxidase.

PGPB can lower ethylene accumulation in plants through the production of "ACC deaminase, an enzyme that cleaves ACC into ammonia and α-ketobutyrate", which can subsequently serve as nitrogen and carbon sources for bacterial metabolism. Through this mechanism, ACC deaminase-producing rhizobacteria decrease stress-induced ethylene levels, alleviate growth inhibition, and promote overall plant development.

Multiple studies confirm that ACC deaminase-producing bacteria counteract ethylene-mediated growth suppression under saline conditions. In tomato, *Achromobacter piechaudii* reduced ethylene production and increased fresh and dry biomass and phosphorus/potassium uptake under 172 mM NaCl (Mayak et al., 2004), while ACC deaminase-deficient *Pseudomonas* mutants produced markedly poorer growth outcomes than wild-type strains in salt-stressed tomato, confirming the causal role of this enzyme (Ali et al., 2014). Halotolerant ACC deaminase-producing strains of *Brevibacterium, Bacillus,* and *Zhihengliuella* supported growth and nutrient uptake in red pepper under salt stress by suppressing ethylene synthesis (Siddikee et al., 2011), and an ACC deaminase-producing *Pseudomonas fluorescens* strain significantly improved salt tolerance and yield in groundnut compared with strains lacking this enzymatic function (Saravanakumar & Samiyappan, 2007). In *Trigonella foenum-graecum*, "ACC deaminase-containing *Bacillus subtilis* reduced

ethylene-induced damage and improved mycorrhizal colonisation and rhizobial nodulation under osmotic stress" (Barnawal et al., 2013).

Beneficial microbes that combine IAA and ACC deaminase production appear to act synergistically: "IAA stimulates cell division and root development, while ACC deaminase" prevents excessive ethylene accumulation, together sustaining plant growth under stress. Co-inoculation of tomato with ACC deaminase- and trehalose-producing *Pseudomonas* sp. UW4 synergistically protected plants against salt stress (Orozco-Mosqueda et al., 2019), and inoculation of salt-stressed chickpea (150 mM NaCl) with the "IAA- and ACC deaminase-producing Pantoea dispersa strain PSB3" improved growth and yield while reducing sodium uptake (Panwar et al., 2016).

2.2.1.3. "Abscisic Acid (ABA)" Modulation

Abscisic acid (ABA) is a key phytohormone in plant adaptation to abiotic and biotic stress, playing a significant role in "tolerance to drought, salinity, and heavy-metal toxicity". Under osmotic stress, ABA is mainly synthesised in roots and transported to aerial tissue, where it regulates stomatal closure, stimulates root growth to enhance water uptake, and helps maintain ionic balance.

PGPB influences endogenous ABA levels and thereby contributes to improved stress tolerance under saline environments. Cucumber inoculated with "*Burkholderia cepacia*, *Promicromonospora* sp., and *Acinetobacter calcoaceticus* under combined salt and drought stress" showed higher biomass, chlorophyll, water status, and downregulation of ABA-associated genes relative to non-inoculated controls (Kang et al., 2014). In soybean, halotolerant rhizobacteria reduced endogenous ABA levels and downregulated the ABA-linked GmNARK signalling pathway, increasing weight, length, and chlorophyll content under NaCl stress (Khan et al., 2019). Similarly, inoculation of maize with Kocuria rhizophila Y1 conferred protection against salinity through coordinated hormonal modulation increased IAA together with reduced ABA associated with downregulation of the ABA-biosynthesis gene ZmNCED1 and altered expression of the ion-transporter genes ZmHKT1 and ZmNHX1-3 (Li et al., 2020).

Other investigations show that specific rhizobacteria can instead increase ABA accumulation, indicating a context-dependent regulatory role. ABA-producing *Bacillus* and *Pseudomonas* strains isolated from grapevine roots reduced water loss and induced ABA accumulation together with defence-related terpene synthesis in *in vitro*-cultured *Vitis vinifera* (Salomon et al., 2014), while an ABA-, IAA-, and gibberellin-producing endophytic "*Azospirillum lipoferum* strain alleviated the effects of osmotic (drought) stress in maize, with ABA" quantitatively confirmed by GC-EIMS (Cohen et al., 2009). Collectively, this body of evidence indicates that PGPB can fine-tune ABA levels in a manner that depends on environmental conditions and host developmental stage, a nuance also emphasised in the broader synthesis by Ilangumaran and Smith (2017).

Table 1

Modulation of phytohormones (IAA, ACC deaminase, ABA) in connection with salinity tolerance (represented by PGPB)

No.	Plant host	Bacterium	Mechanism	Effect	Citation
1	*Gossypium hirsutum* L.	*Pseudomonas putida* Rs-198	IAA production; ABA suppression	Increased germination rate, productivity traits, nutrient content	Yao et al. (2010)
2	*Arachis hypogaea* L.	*Brachybacterium, Brevibacterium, Haererohalobacter* spp.	Water homeostasis; IAA accumulation	Higher productivity traits and nutrient content) (100 mM NaCl	Shukla et al. (2012)

3	*Triticum aestivum* L.	*Streptomyces* sp.	IAA and siderophore production	Increased germination, seedling length, weight, nutrient content	Sadeghi et al. (2012)
4	*Phaseolus vulgaris* L.	*Azospirillum brasilense* + *Rhizobium etli*	IAA production	Higher root weight, root number, and nodulation	Remans et al. (2008)
5	*Zea mays* L.	*Pseudomonas fluorescens* + *Enterobacter aerogenes*	ACC deaminase production	Increased height, biomass, K+/Na+ ratio, NPK uptake	Zahir et al. (2012)
6	*Trigonella foenum-graecum* L.	*Bacillus subtilis*	ACC deaminase production	Reduced ethylene damage; improved nodulation/mycorrhization under osmotic stress	Barnawal et al. (2013)
7	*Solanum lycopersicum* L.	*Achromobacter piechaudii*	ACC deaminase production	Increased fresh/dry weight, P and K uptake (172 mM NaCl)	Mayak et al. (2004)
8	*Capsicum annuum* L.	*Brevibacterium, Bacillus, Zhihengliuella* spp.	ACC deaminase production	Higher biomass and nutrient uptake (halotolerant strains)	Siddikee et al. (2011)
9	*Arachis hypogaea* L.	*Pseudomonas fluorescens*	ACC deaminase production	Increased seedling weight, height, germination	Saravanakumar & Samiyappan (2007)
10	*Solanum lycopersicum* L.	*Pseudomonas* sp. UW4	ACC deaminase + trehalose production	Synergistic protection: root/shoot length, dry weight, chlorophyll	Orozco-Mosqueda et al. (2019)
11	*Solanum lycopersicum* L.	*P. fluorescens / P. migulae* (ACC-deaminase mutants)	ACC deaminase production	Wild type > mutant for biomass, chlorophyll, flowering	Ali et al. (2014)
12	*Cicer arietinum* L.	*Pantoea dispersa* (PSB3)	IAA + ACC deaminase production	Improved yield, K+/Na+ ratio, water/chlorophyll content (150 mM NaCl)	Panwar et al. (2016)
13	*Cucumis sativus* L.	*Burkholderia, Promicromonospora, Acinetobacter* spp.	Downregulation of ABA-associated genes	Increased biomass, chlorophyll, K/P content under salt + drought	Kang et al. (2014)
14	*Glycine max* L.	*Halotolerant rhizobacteria (Bacillus/Arthrobacter* spp.*)*	Reduced ABA; downregulation of GmNARK	Increased fresh/dry weight, length, chlorophyll content	Khan et al. (2019)
15	*Zea mays* L.	*Kocuria rhizophila Y1*	HKT/NHX and ZmNCED1 gene regulation; IAA up, ABA down	Decreased Na+ accumulation; improved productivity traits	Li et al. (2020)
16	*Vitis vinifera* L.	*Bacillus* sp. + *Pseudomonas* sp.	ABA production/accumulation	Reduced water-loss rate; terpene defence synthesis	Salomon et al. (2014)
17	*Zea mays* L.	*Azospirillum lipoferum*	ABA, IAA, gibberellin production	Reversed effects of osmotic (drought) stress	Cohen et al. (2009)

This is a compilation of the authors from the primary studies mentioned in the final (Citation) column of the above table.

2.3. Ion Toxicity

Saline conditions cause the build-up of certain ions, primarily sodium (Na+) and chloride (Cl−) in the plant tissue (Tester & Davenport, 2003). Excessive absorption of these ions affects enzyme function, compromise membrane integrity and interfere with nutrient absorption, particularly "potassium (K^+) and calcium (Ca^{2+}) which are essential for protein synthesis and membrane" function. Common symptoms of ion toxicity are chlorosis, marginal necrosis and early senescence, especially on older leaves where accumulation of salts occurs.

2.4. Impairment of Photosynthesis and Growth

2.4.1. Reduced Photosynthetic Efficiency

Salinity stress affects photosynthesis by disrupting the activity of enzymes in the Calvin cycle, causing damage to the chlorophyll pigments, and damaging Photosystem II. The osmocosmosis also leads to reduced stomatal conductance which further limits the supply of CO_2 to the chloroplasts, thus further reducing the photosynthetic rate.

2.4.2. Reduced Growth and Biomass

The amount of carbohydrates produced by the plants for energy and plant structure is reduced due to less photosynthetic carbon fixing. The growth inhibition is most severe in young rapidly growing tissue (leaf tips and root tips) and the resulting decrease in assimilate production has a negative impact on both vegetative and reproductive growth, resulting in a reduction in yield.

2.5. Altered Gas Exchange

2.5.1. Stomatal Closure

When exposed to salinity, "plants close their stomata to conserve water", so less water transpires and less salt is taken up. This adaptive response is a mechanism to cope with high salinity under water limitation and is involved in maintaining water homeostasis and ion homeostasis in the cell.

2.5.2. Diffusion of Nutrients is Also Lowered and Transpiration is Reduced

Persistent stomatal closure causes reduced transpiration, which causes reduction in evaporative cooling and in the transport of nutrients in the xylem, thus increasing the deficiency of essential minerals like N, P and K, and hence further compromising the metabolic activity (Ilangumaran & Smith, 2017; Alhan et al., 2026).

2.6. Metabolic Changes & Excess Production of Reactive Oxygen Species (ROS)

2.6.1. Oxidative Stress

Overproduction "of reactive oxygen species (ROS) like superoxide radicals (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radicals (·OH) in chloroplast, mitochondria, and" peroxisome all frequently accompany salinity stress. High levels of ROS can cause genetic damage, inactivate enzymes, and result in membrane leakage (Ilangumaran & Smith, 2017; Alhan et al., 2026).

2.6.2. The Disruption of Key Metabolic Pathways

Ionic imbalance and oxidation damage affect the most important metabolic functions such as respiration, nitrogen assimilation and hormone signal transduction. These hormonal changes, including elevated ABA and decreased levels of cytokinin, alter stress-signalling pathways and gene expression and either promote short-term survival or limit further growth (Ilangumaran & Smith, 2017; Alhan et al., 2026).

3. The Most Important "Mechanisms of Salinity Tolerance Induced by PGPB"

"The effects of salinity on physiology outlined above causes substantial losses in crop yields. But the positive effects of PGPB have been demonstrated to enhance crop growth and to reduce the adverse effects of high soil" populations. This beneficial effect is achieved by several mechanisms such as maintaining ionic balance, synthesis of stress-relieving phytohormones and improvement in nutrient-uptake efficiency. PGPB also plays a role in antioxidant enzyme activation and osmotic adjustment, which helps the plants cope with oxidative stress and cellular damage (Ilangumaran & Smith, 2017; Alhan et al., 2026).

3.1. Water Homeostasis and Accumulation of Osmolytes "To Maintain Osmotic Balance"

"Under salinity conditions, the initial physiological stress which is experienced by plants is osmotic stress. It disrupts water balance causing stomatal closure and a decrease in photosynthetic activity and gas exchange"; carbohydrate accumulation is stored in meristems and storage tissue instead of new-tissue growth, limiting plant proliferation and expansion.

In order to survive, "plants need to regulate water homeostasis and to protect the photosynthetic structures". PGPB acts in various ways to contribute to osmotic balance. The other pathway is through bacterial extracellular polysaccharide (EPS) complex, which is high-molecular weight carbohydrate producing protective biofilm around roots, which retain water in soil, improves soil structure and reduces the Na^+ uptake (Shahid et al., 2026). PGPB may also trigger the plant to produce endogenous plant osmolytes "proline, glycine betaine and soluble sugars as molecular chaperones that help in the stability of protein and cellular structures and turgor pressure. This dual physical barrier/ biochemical adjustment approach is of help to plants in the first stage when they are exposed to saline conditions. In addition, EPS" also works by binding particles together, which is essential for good soil aggregation, thereby increasing soil porosity and aeration, which is required for root growth.

Under field condition, co-inoculation of lettuce with Pseudomonas mendocina and arbuscular mycorrhizal fungus Glomus intraradices improved soil aggregate stability due to increased EPS production (Kohler et al., 2006), while Halomonas variabilis–Planococcus rifietensis improved the growth of chickpea and soil aggregation under salinity stress by increasing EPS and biofilm production (Qurashi & Sabri, 2012). EPS-producing rhizobacteria have similarly improved wheat growth and selective nutrient uptake under salt stress (Ashraf et al., 2004; Talebi Atouei et al., 2019), while co-inoculation of *alfalfa* with *Halomonas maura* and *Ensifer meliloti* increased plant biomass and leghemoglobin content through combined nodulation and EPS effects (Martínez et al., 2015), and indigenous EPS-producing rhizobacteria improved productivity traits and the K^+/Na^+ ratio in pistachio seedlings under salinity and drought (Khalilpour et al., 2021).

Salinity-induced growth reduction is also linked to "feedback inhibition of photosynthesis, and microorganisms help modulate the source-sink relationship of soluble sugars, supporting osmotic adjustment" during the osmotic phase of salinity. In Medicago ciliaris, salt tolerance conferred by *Sinorhizobium medicae* was linked to maintenance of source-sink carbohydrate and hormonal relationships during symbiotic nodulation (Ben Salah et al., 2012), and "co-inoculation of soybean with *Bradyrhizobium japonicum* 532C, *Rhizobium sp*. SL42, and *Hydrogenophaga* sp. SL48 enhanced shoot and root growth, nitrogen assimilation, and the K^+/Na^+ ratio" through improved symbiotic nodulation and source-sink balance (Ilangumaran et al., 2021). In pepper, co-inoculation with *Azospirillum brasilense* and *Pantoea dispersa* under 40-120 mM NaCl improved yield-related traits via "enhanced stomatal conductance and photosynthesis (Del Amor & Cuadra-Crespo, 2012), and inoculation with various *Bacillus* strains has similarly improved photosynthesis, stomatal conductance, productivity, and fruit quality in strawberry" (Karlidag et al., 2013).

"Plants accumulate compatible solutes commonly termed osmolytes, such as proline, glycine betaine, and trehalose" to counter osmotic imbalance. PGPB frequently synthesise osmoregulators more rapidly than plants themselves and can enhance host osmolyte content either through direct uptake of bacterial solutes or by stimulating de-novo synthesis in plant tissue. Trehalose-accumulating *Azospirillum brasilense* improved "biomass and survival in maize under water-deficit stress" (Rodríguez-Salazar et al., 2009), and osmolyte-accumulating *Bacillus* spp. together with *Paenibacillus favisporus* enhanced maize biomass, water homeostasis, and soil aggregate stability under drought-related osmotic stress (Vardharajula et al., 2011). "Co-inoculation of maize with *Rhizobium* sp. and *Pseudomonas* sp." enhanced development, biomass, and nutrient uptake through combined proline accumulation and ion/water homeostasis (Bano & Fatima, 2009), while combined endophytic and rhizospheric inoculation of rice with *Pseudomonas pseudoalcaligenes* and *Bacillus pumilus* increased plant weight and height through elevated osmoprotectant accumulation (Jha et al., 2011; Zahir et al., 2012).

Wheat inoculated with the halotolerant, osmoprotectant-accumulating strain *Bacillus aquimaris* showed increased biomass, weight, and leaf-nutrient content under saline soil (Upadhyay & Singh, 2015), while inoculation with "*Bacillus megaterium* MPP7, *Bacillus tequilensis* MPP8, and *Pseudomonas putida* MPP18 reduced electrolytic leakage and oxidative damage" through combined proline/soluble-sugar accumulation and transcriptional upregulation of the SOS-type ion-transporter genes SOS1 and SOS4 (Haroon et al., 2022). Comparable benefits from osmolyte accumulation have been reported in peak inoculated with *Acinetobacter, Enterobacter*, and *Alcaligenes* strains, where elevated osmolyte levels correlated with reduced oxidative damage (Sapre et al., 2022).

Beyond biochemical modulation, PGPB also regulates plant water homeostasis through effects on hydraulic conductivity. *Bacillus megaterium* B26 "enhanced salt-stress tolerance in maize through positive regulation of PIP-type aquaporin genes and improved root hydraulic conductance (Marulanda et al., 2010), and *Azospirillum brasilense* increased aquaporin gene transcription and improved growth in barley seedlings exposed to saline stress (Zawoznik et al., 2011)". The results altogether demonstrate PGPB activate several complementary mechanisms, including osmotic modulation, enhancement of antioxidant defence, and hydraulic regulation, which significantly enhance plant's resistance in saline soil.

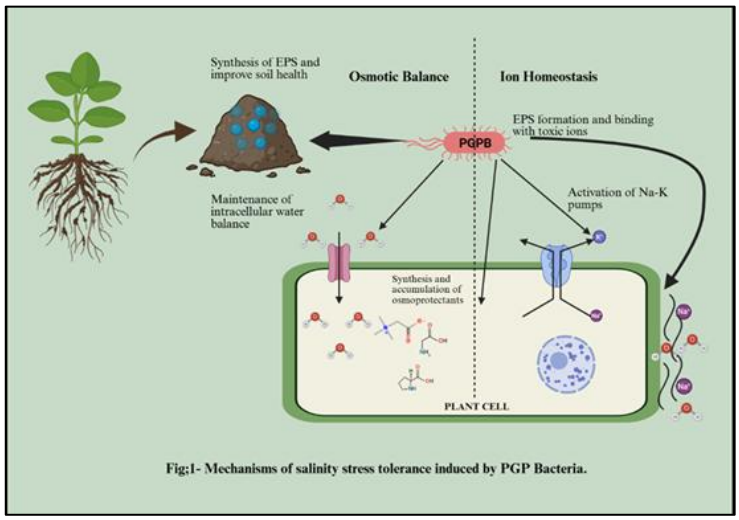


Figure 2

"Main mechanisms of salinity tolerance induced by plant growth-promoting bacteria" (PGPB): Complementary role in osmotic balance (EPS synthesis, accumulation of osmoprotectants, maintenance of water balance in cell) and ion homeostasis (EPS binding of toxic ions, activation of Na^+/K^+ pumps).

Figure source. Original figure prepared by the authors and synthesised from the mechanistic evidence discussed in Section 3.1-3.2 that was analysed in the primary studies cited (Ilangumaran & Smith, 2017).

Table 2
Biological processes mediated by Rep PGPB to maintain osmotic balance and control of ion homeostasis related to salinity tolerance

No.	Plant host	Bacterium	Effect	Mechanism	Citation
1	*Lactuca sativa* L.	*Pseudomonas mendocina (+ Glomus intraradices)*	Increased stable soil aggregation	EPS production	Kohler et al. (2006)
2	*Cicer arietinum* L.	*Halomonas variabilis + Planococcus rifietensis*	Increased growth and soil aggregation under salinity	Biofilm formation and EPS production	Qurashi & Sabri (2012)
3	*Medicago ciliaris* L.	*Sinorhizobium medicae*	Differential carbohydrate/hormonal changes between source-sink tissues	Nodulation and source-sink activity	Ben Salah et al. (2012)
4	*Glycine max* L.	*B. japonicum* 532C, *Rhizobium* sp. SL42, *Hydrogenophaga* sp. SL48	Improved shoot/root growth, N assimilation, K+/Na+ ratio	Nodulation and source-sink activity	Ilangumaran et al. (2021)
5	*Capsicum annuum* L.	*Azospirillum brasilense + Pantoea dispersa*	Higher dry weight and K+/Na+ ratio (40-120 mM NaCl)	Higher stomatal conductance/transpiration	Del Amor & Cuadra-Crespo (2012)
6	*Fragaria x ananassa*	*Bacillus licheniformis, B. subtilis, Bacillus* sp.	Enhanced growth, yield, fruit quality	Higher stomatal conductance/transpiration	Karlidag et al. (2013)
7	*Triticum aestivum* L.	*Bacillus aquimaris*	Increased biomass, weight, leaf nutrients	Osmoprotectant accumulation (proline, soluble sugar)	Upadhyay & Singh (2015)
8	*Zea mays* L.	*Azospirillum brasilense*	Increased survival, leaf/root biomass	Trehalose accumulation "water-deficit stress"	Rodríguez-Salazar et al. (2009)
9	*Zea mays* L.	*Bacillus spp. + Paenibacillus favisporus*	Increased biomass, water homeostasis, soil-aggregate stability	Osmoprotectant accumulation (proline, sugar)	Vardharajula et al. (2011)
10	*Zea mays* L.	*Rhizobium* sp. + *Pseudomonas* sp.	Enhanced development, biomass, nutrient uptake	Proline accumulation; ion/water homeostasis	Bano & Fatima (2009)
11	*Oryza sativa* L.	*Pseudomonas pseudoalcaligenes*	Higher plant weight and height	Osmoprotectant accumulation (glycine betaine-like compounds)	Jha et al. (2011)

		+ *Bacillus pumilus*			
12	*Triticum aestivum* L.	*B. megaterium* MPP7, *B. tequilensis* MPP8, *P. putida* MPP18	Reduced electrolytic leakage and oxidative damage	Osmoprotectant accumulation; SOS1/SOS4 transcriptional upregulation	Haroon et al. (2022)
13	*Pisum sativum* L.	*Acinetobacter, Enterobacter, Alcaligenes* spp.	Reduced oxidative damage	Osmoprotectant accumulation (proline, soluble sugar)	Sapre et al. (2022)
14	*Zea mays* L.	*Bacillus megaterium* B26	Higher root hydraulic conductance	Upregulation of PIP-type aquaporin genes	Marulanda et al. (2010)
15	*Hordeum vulgare* L.	*Azospirillum brasilense*	Increased biomass and height	Upregulation of PIP-type aquaporin genes	Zawoznik et al. (2011)
16	*Triticum aestivum* L.	*Aeromonas* sp. + *Bacillus* sp.	Increased growth, K+/Na+ ratio, soil aggregation	EPS production	Ashraf et al. (2004)
17	*Triticum aestivum* L.	*Bacillus subtilis* + *Marinobacter lipolyticus*	Increased growth, K+/Na+ ratio, selective nutrient uptake	EPS production	Talebi Atouei et al. (2019)
18	*Lactuca sativa* L.	*Pseudomonas mendocina*	Increased biomass and water content (water stress)	Phosphatase activity; proline accumulation	Kohler et al. (2008)
19	*Medicago sativa* L.	*Halomonas maura* + *Ensifer meliloti*	Increased plant biomass and leghemoglobin	Nodulation and EPS production	Martínez et al. (2015)
20	*Pistacia vera* L.	*Staphylococcus sciuri, Zobellella denitrificans, Arthrobacter endophyticus*	Increased productivity traits and K+/Na+ ratio	EPS production	Khalilpour et al. (2021)

This data was compiled by the authors from the studies in the primary data column identified in the last column (Citation) of the table above.

3.2. Homeostasis-Ion Homeostasis (The Regulation of Ions)

Salinity causes the accumulation of ions (Na+, Cl-, Ca2+, Mg2+, SO42-, and CO32-) and results in an ion toxicity stage when the plant is no longer able to exclude the ions. As one of the initial protective responses, plants sequester excess salts into vacuoles with no accumulation in other compartments, such as cytosol that would otherwise interfere with photosynthesis and respiration. High levels of Na^+ affect K^+-dependent processes because biochemical reactions that involve K^+ are affected by substituting K^+ with Na^+ which alters protein structure and synthesis. There is a clear relationship between productivity and ionic equilibrium, mostly studied in relation to salinity imposed by NaCl, but soil microorganisms play a role in maintaining ionic equilibrium and hence improve growth and salinity tolerance, particularly for other ions that cause salinity stress (Tester & Davenport, 2003).

Maintenance of high K^+/Na^+ ratio is one of the important PGPB mechanisms that involves "reducing the accumulation of Na^+/Cl^- in leaves, stimulation of ion exclusion at the root surface, or regulation of the expression of genes encoding ion transporters. High-affinity K^+ transporters (HKT) are" important in limiting excessive Na^+ accumulation in the shoot by exporting Na^+ to the roots. In Puccinellia tenuiflora, the halophyte grass, the salt tolerance was enhanced by the inoculation with Bacillus subtilis GB03, which promoted selective K^+ uptake over Na^+, inhibited the root and shoot growth and expression of the HKT1 and HKT2 genes (Niu et al., 2016). In the case of maize, inoculation with Kocuria rhizophila Y1 led to the increased expression of HKT1, NHX1, NHX2 and NHX3 genes, which resulted in higher salt tolerance and protection against salt (Li et al., 2020).

Sodium antiporters, which are encoded by Salt Overly Sensitive (SOS) genes are also important in salinity tolerance besides the HKT transporters. Wheat was stressed with salt and then inoculated with Bacillus megaterium, Bacillus tequilensis, and Pseudomonas putida, which led to an induction of expression of SOS1 and SOS4, which was associated with an improvement in the relative water content and an increase in the photosynthetic pigments (Haroon et al., 2022).

PGPB also help reduce the buildup of Na^+/Cl^- by controlling macro- and micronutrient exchange. The production of proteins associated with phosphatase activity can be stimulated by PGPB inoculation, and by microbial phosphate solubilisation and siderophore production, nutrient availability can be improved. Pseudomonas simiae AU under saline stress conditions promoted the expression of vegetative storage protein (VSP) which play an important role in the acid-phosphatase activity along with increase in weight, length and K^+/Na^+ ratio in soybean (Vaishnav et al., 2015) while under water stress condition, Pseudomonas mendocina colonized lettuce and resulted into increased acid-phosphatase activity and reduced oxidative stress (Kohler et al., 2008). Azotobacter chroococcum strains inoculated in maize increased the exclusion of Na ions and improved the uptake of K ions as well as the polyphenol/chlorophyll content, compared to plants not inoculated with A. chroococcum (Rojas-Tapias et al., 2012).

Production of exopolysaccharides (EPS) is another important microbial mechanism that can help mitigate the toxicity of ions by building up a protective physical barrier around the root system, which sequesters cations like Na^+ which are harder to take up by "the root system and reduces the movement of these ions to the aerial parts of the plant". The EPS-producing rhizobacteria have shown positive effects on wheat growth and changed the nutrient uptake in saline soils, with reduced uptake of Na^+ and increased uptake of K^+/Ca^{2+} (Ashraf et al., 2004; Talebi Atouei et al., 2019), and similar effects have been seen with soybean, alfalfa and pistachio (Martínez et al., 2015; Khalilpour et al., 2021).

4. Other Bioactive Molecules from Rhizobacteria which are Affecting Plant Health

There are several bacterial mechanisms of plant salt stress regulation that include the release of extracellular metabolites such as volatile organic compounds and low molecular weight organic substances. These compounds are molecules that are involved in the process of signalling between organisms, regulating plant processes, and creating beneficial physiological responses in plants under stressful conditions.

4.1. Volatile Organic Compounds (VOCs) Emission

The "Volatile Organic Compounds (VOCs) are low molecular weight, carbon-based chemicals with high vapour pressure and low boiling point which can be emitted by rhizosphere associated bacteria. Microbial volatiles have been reported to promote plant growth and protect against phytopathogens, and" growing evidence suggests their ability to alleviate salt stress.

Under 100 mM NaCl, exposure to the VOC mixture produced by Pseudomonas simiae resulted in decreased sodium concentrations in the root tissue and increased proline and chlorophyll content,

while associated changes in induced protein expression were observed (Vaishnav et al., 2015) in another study, the VOCs 4-nitroguaiacol and quinoline were specifically found to enhance soybean seed germination under the same salt concentration (Vaishnav et al., 2016). In Mentha x piperita VOCs produced by Bacillus amyloliquefaciens GB03, with acetoin as the major compound, offset the negative effects of salt stress over the entire range of NaCl tested (0–100 mM), and were correlated with a decrease in endogenous ABA levels, indicating a possible hormonal mechanism of action (Cappellari & Banchio, 2020).

4.2. Biosynthesis of Polyamines

Small aliphatic amines known as polyamines (PAs) have a potent antioxidant potential and "are essential for plant growth, development, and the response to abiotic stress". They also control gene expression, antioxidant enzyme activity, and ROS homeostasis. The three most common physiologically active forms found in plants are putrescine, spermidine, and spermine.

Comparatively few studies have examined polyamines produced directly by PGPB. Spermidine secreted by *Bacillus amyloliquefaciens* SQR9 mitigated oxidative damage, limited sodium toxicity, and suppressed ABA accumulation in *Zea mays*, an effect further validated using polyamine-deficient bacterial mutants (Chen et al., 2017). In tomato, *Bacillus megaterium* TG1-E1 elevated extracellular arginine a key polyamine precursor under hyperosmotic stress, suggesting that bacterial inoculation may indirectly enhance endogenous polyamine synthesis and contribute to improved stress resilience (Morcillo et al., 2021).

4.3. Production of Lipo-Chito-Oligosaccharides and Bacteriocins

"Bacteriocins are ribosomally synthesised antimicrobial peptides with bactericidal or bacteriostatic activity against closely related" microbial species, effective at very low concentrations and providing producing bacteria with a competitive advantage in the rhizosphere.

Lipo-chito-oligosaccharides (LCOs) are microbial signalling molecules that initiate and regulate symbiotic interactions with plants; the best-known group, "Nod factors, are released by rhizobacteria in response to root-exudate flavonoids" and are central to root-nodule initiation in legumes. Beyond symbiosis, nod factors also positively influence plant growth under abiotic stress. "Thuricin 17, a bacteriocin produced by *Bacillus thuringiensis* NEB17", combined with LCOs from *Bradyrhizobium japonicum* 532C, enhanced canola (*Brassica napus*) accumulation and root development under stress conditions (Schwinghamer et al., 2016). Proteomic analysis of the same Thuricin 17 + *B. japonicum* 532C LCO combination applied to soybean under 100 mM NaCl revealed substantial reprogramming of proteins associated with photosynthesis, primary metabolism, and stress defence, including PEP carboxylase, the large subunit of Rubisco, glutathione-S-transferase, and late embryogenesis abundant (LEA) proteins linked to dehydration tolerance (Subramanian et al., 2016). In total, these results suggest that the plant proteome can be reprogrammed by bacteriocins and LCOs, as well as improving its physiological tolerance to salinity stress.

Table 3

Representative compounds produced by PGPB were volatile organic compounds, polyamines, and bacteriocins/lipo-chito-oligosaccharides associated with salinity tolerance

No.	Plant host	Bacterium	Mechanism	Effect	Citation
1	*Glycine max* L.	*Pseudomonas simiae*	VOC production; phosphatase-activity changes	Higher weight/length, K+/Na+ ratio "100 mM NaCl"	Vaishnav et al. (2015)

2	*Glycine max* L.	*P. simiae (4-nitroguaiacol, quinoline)*	VOC production	Promoted seed germination “100 mM NaCl"	Vaishnav et al. (2016)
3	*Mentha x piperita* L.	*Bacillus amyloliquefaciens* GB03	VOC production (acetoin); reduced ABA	Higher chlorophyll and improved morphology	Cappellari & Banchio (2020)
4	*Zea mays* L.	*Bacillus amyloliquefaciens* SQR9	Polyamine (spermidine) production	Decreased oxidative/Na+ damage; ABA suppression	Chen et al. (2017)
5	*Solanum lycopersicum* L.	*Bacillus megaterium* TG1-E1	Arginine (polyamine-precursor) accumulation	Osmotic-stress resistance	Morcillo et al. (2021)
6	*Brassica napus* L.	*B. thuringiensis NEB17* + *B. japonicum* 532C	Bacteriocin (Thuricin 17) + LCO production	Enhanced biomass and root development under stress	Schwinghamer et al. (2016)
7	*Glycine max* L.	*B. thuringiensis NEB17* + *B. japonicum* 532C	Bacteriocin (Thuricin 17) + LCO production	Proteome reprogramming “under 100 mM NaCl”	Subramanian et al. (2016)

The source is the authors' compilation based on the primary studies mentioned in the last column (Citation) of the table.

5. Conclusion

Soil salinity is an important and global problem that adds multiple stresses to plants: “osmotic stress, ion toxicity, nutrient stress, and oxidative stress, and can also decrease the soil structure and fertility. In this context, the idea of using plant growth-promoting bacteria has” proven to be a promising strategy that is sustainable and economically viable to enhance plant resistance to salinity. There are several physiological and biochemical mechanisms that contribute to PGPB mediated salt-stress tolerance, e.g., modulation of phytohormone balance (IAA, ABA) along with inhibition of the ethylene production pathway by ACC deaminase, secretion of signalling molecules and bioactive metabolites (lipo-chito-oligosaccharides, polyamines, VOCs, EPSs), activation of ion-transport systems, and “accumulation of osmoprotectants (proline, trehalose, soluble sugars)”.

“Despite significant advances, the complexity of plant-microbe interactions” and the diversity of microbial functional traits remain insufficiently understood. The synergistic and context-dependent nature of PGPB mechanisms evident, for example, in strain- and host-dependent ABA modulation necessitates deeper investigation to unravel their coordinated roles under field conditions. Variability in microbial performance across crops and environmental settings further highlights the need for targeted screening and functional characterisation of halotolerant strains, and for validated multi-strain consortia and engineered microbiomes rather than single-strain inoculants alone.

In conclusion, harnessing the full potential of PGPB represents a transformative approach for sustainable agriculture in salt-affected soils. Future research should prioritise integrative multi-omics approaches, rational design of microbial consortia, CRISPR-enabled functional genomics of stress-

tolerance pathways, and long-duration, multi-location field-level validation to bridge the gap between laboratory findings and practical application. Such advances will be pivotal for developing climate-resilient cropping systems and ensuring long-term global food security.

Statement of credit authorship contribution

SRK: Writing–original draft, Literature survey, Formal analysis, data compilation, Software, Investigation**. SS:** Writing–review & editing, Supervision. **IA**: Writing–review & editing, Supervision, Investigation. **FAA**: Writing–review & editing, Supervision. **SK**: Literature survey, Software, Resources.

A statement of conflicting interests

The authors affirm that none of the work reported in this review could have been influenced by any known competing financial interests or personal relationships. **FAA** is a member of the journal's Editorial Board and was not involved in the editorial evaluation or publication decision concerning this manuscript.

Acknowledgements

The Integral Institute of Agricultural Science and Technology, Integral University, Lucknow, as well as the affiliated institutions of all co-authors, are acknowledged by the authors for providing institutional and infrastructure support during the production of this review.

Data availability

Not applicable

Funding

This research received no external funding from any funding agency in the public, commercial, or non-profit sectors.

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