Role of exopolysaccharides (EPS) in salt stress tolerance

Sharda Yadav, Swati Yadav and Renu Varma*
Department of Biotechnology, Faculty of Engineering & Technology,
Rama University, Mandhna, Kanpur, Uttar Pradesh
*Email: renuverma.fet@ramauniversity.ac.in

Abstract

Soil salinization has emerged as one of the most damaging environmental constraints facing modern agricultural systems, with an estimated 20% of irrigated farmland currently impaired by excessive salt accumulation. Among the diverse biological strategies that have attracted scientific attention, exopolysaccharides (EPS) produced by plant growth-promoting rhizobacteria (PGPR) represent a particularly promising avenue. These high-molecular-weight biopolymers, secreted into the immediate surroundings of bacterial cells, fulfill a multitude of functions ranging from soil particle binding and water retention to direct ionic buffering and the modulation of plant physiological responses. This review synthesizes current knowledge on EPS structure, biosynthesis pathways, and the mechanistic roles these molecules play in alleviating salt stress in crop plants. We observe how EPS production is upregulated under saline conditions, how the resulting polymers modify soil physical properties, and how EPS-producing bacteria communicate with and protect host plants through phytohormone signaling, reactive oxygen species (ROS) scavenging, and selective ion exclusion. Evidence from controlled greenhouse trials as well as field-scale experiments is evaluated critically, including instances where published findings appear contradictory. This concludes by identifying key research gaps and proposing directions for the practical deployment of EPS-producing bacteria in saline agriculture. this work aims to provide an agronomists, microbiologists, and plant physiologists seeking to leverage microbial biotechnology for sustainable crop production under salt stress.

Keywords: Exopolysaccharides, Salt Stress, PGPR, Rhizobacteria, Soil Aggregation, Biofilm, Ion Exclusion

1. Introduction

Salinity is now widely recognized as a principal abiotic stressor that limits crop productivity on a global scale (Munns & Tester, 2008; Zhu, 2016). Soils with electrical conductivity exceeding 4 ds m^{-1} are classified as saline, and such conditions currently affect more than 800 million hectares worldwide (Parida & Das, 2005; Mahajan & Tuteja, 2005). The problem is not static; rising irrigation demands, inadequate drainage infrastructure, and the intensifying effects of climate change are expected to push an additional 50% of arable land into the saline category by 2050 (Raza et al., 2019). At the cellular level, salinity imposes two overlapping stresses: an osmotic component that restricts water uptake even before toxic ions accumulate in

tissues, and an ionic component arising from the progressive buildup of Na^+ and Cl^- to concentrations that interfere with enzyme function, membrane integrity, and photosynthetic efficiency (Munns, 2002; Zhu, 2003).

Conventional plant breeding has delivered incremental gains in salinity tolerance, but the polygenic and quantitative nature of this trait makes rapid progress difficult (Dodd & Pérez-Alfocea, 2012). Chemical ameliorants such as gypsum or organic matter applications can improve saline soil structure, yet their cost and logistical demands render them impractical in many developing regions (Ilangumaran & Smith, 2017). Against this backdrop, the use of salt-tolerant PGPR that secrete biologically active exopolysaccharides has gained considerable traction as a low-cost, ecologically compatible intervention (Upadhyay et al., 2011; Etesami & Beattie, 2018).

Exopolysaccharides are complex, water-soluble polymers released by bacteria into their extracellular milieu (Flemming & Wingender, 2010). Their chemical diversity is remarkable: they may be homo or heteropolysaccharides, neutral or acidic, linear or branched, and their molecular weights can span from tens of thousands to several million Daltons (Laspidou & Rittmann, 2002). Well-studied examples include xanthan from *Xanthomonas campestris*, *levan* from *Bacillus subtilis*, *alginate* from *Azotobacter vinelandii*, and *succinoglycan* from *Sinorhizobium meliloti* (Deinema & Zevenhuizen, 1971; Hepper, 1975). In saline soils, the anionic character of many EPS molecules allows them to bind Na^+ ions, reducing the concentration of free sodium available for plant root uptake (Ashraf et al., 2004; Qurashi & Sabri, 2012). Simultaneously, their hygroscopic gel-like matrix stabilizes soil aggregates and maintains the moisture microenvironment around roots, partially counteracting the osmotic penalty imposed by salt (Alami et al., 2000; Chenu, 1993).

Despite the rapid growth of the literature in this area, a coherent and critical synthesis remains lacking. Published studies vary widely in their experimental designs differing salt concentrations, plant species, bacterial strains, inoculation methods, and assessment time points making cross-study comparisons difficult. Furthermore, certain reported outcomes appear contradictory while many studies demonstrate dose-dependent benefits of EPS on plant growth at moderate salinity, a smaller but non-trivial body of evidence points to neutral or occasionally negative outcomes at extreme ionic concentrations or when incompatible plant–bacterium pairs are tested (Tewari & Arora, 2014; Nookongbut et al., 2019). The

present review addresses these inconsistencies systematically, with the goal of providing a nuanced, evidence-based understanding of EPS-mediated salt stress mitigation.

The objectives of this review are: (1) to describe the structural diversity and biosynthetic regulation of bacterial EPS under salt stress; (2) to detail the soil-level and plant-level mechanisms through which EPS alleviates salinity damage; (3) to evaluate experimental evidence from key studies; (4) to highlight contradictions in the literature and suggest explanations; and (5) to outline priorities for future research and agronomic application (Meena et al., 2017; Oleńska et al., 2020).

2. Global Impact of Soil Salinity on Agriculture

The agricultural footprint of soil salinity is staggering. Primary salinity, arising from natural mineral weathering and capillary rise of saline groundwater, has shaped the soil chemistry of arid and semi-arid regions for millennia. Secondary salinity, driven by human activities such as over-irrigation and poor drainage management, is the more pressing contemporary concern (Parida & Das, 2005; Manchanda & Garg, 2008). In South Asia, for example, saline soils reduce rice and wheat yields by an average of 30–40%, with localized losses reaching complete crop failure in severely affected plots (Fahad et al., 2015). Sub-Saharan Africa, the Middle East, and Central Asia face comparable challenges, and even temperate cropping systems are not immune as irrigation intensity increases (Dotto & Casanova, 2010).

The economic toll is equally sobering. Globally, salinity-induced losses in agricultural productivity are estimated to exceed USD 12 billion annually, a figure that does not capture the broader socioeconomic consequences of food insecurity and rural poverty in salt-affected regions (Raza et al., 2019; Meena et al., 2017). Reclaiming salt-damaged soils through physical or chemical means is possible but expensive; the installation of subsurface drainage systems alone can cost USD 1,000–3,000 per hectare. Biological approaches, including the inoculation of crops with EPS-producing bacteria, can in contrast often be implemented for a fraction of this cost while simultaneously building soil microbial capital (Bhattacharyya & Jha, 2012).

The physiological basis of salt damage in crops involves multiple intersecting pathways. Ion toxicity accumulates as Na^+ competes with K^+ for transporter binding sites, impairing enzymatic reactions that depend on adequate K^+ availability (Zhu, 2003). The resulting nutritional imbalance

compounds the osmotic deficit already created by reduced soil water potential, and together these stresses suppress cell expansion, leaf development, and grain filling (Munns, 2002; Munns & Tester, 2008). Reactive oxygen species generated under ionic stress further damage membranes, proteins, and nucleic acids, accelerating senescence and reducing harvestable biomass (Evelin et al., 2009; Parida & Das, 2005).

3. Exopolysaccharides: Definition, Structure, and Biosynthesis

3.1 Structural Diversity of Bacterial EPS

Bacterial exopolysaccharides are defined as polysaccharides synthesized intracellularly and exported to the cell exterior, where they may remain attached as a capsule or be released as a loose slime into the surrounding medium (Flemming & Wingender, 2010; Laspidou & Rittmann, 2002). Their structural diversity reflects the enormous taxonomic breadth of EPS producing bacteria. Homopolysaccharides such as dextran (a polymer of glucose), levan (fructose units), and cellulose (β-1,4-glucose) are found in numerous soil isolates. More commonly encountered in rhizobacterial genera are heteropolysaccharides composed of repeating oligosaccharide units that incorporate two or more sugar types along with non-carbohydrate substituents such as acetyl, pyruvyl, or succinyl groups (Deinema & Zevenhuizen, 1971; Hepper, 1975).

The acidic character of many EPS molecules is conferred by uronic acid residues particularly glucuronic and galacturonic acid as well as by pyruvate ketal and acetate groups on the sugar backbone. This negative charge is pivotal for cation binding, which underlies many of the salt-ameliorating properties of EPS (Chenu, 1993; Qurashi & Sabri, 2012). The three-dimensional conformation adopted by EPS chains commonly described as coil, helix, or gel-forming network further dictates viscosity, water-holding capacity, and adhesion properties (Flemming & Wingender, 2010). Succinoglycan, produced by *Sinorhizobium meliloti*, exemplifies an EPS that forms stable gel networks capable of retaining many times their dry weight in water, an attribute directly relevant to moisture conservation in saline soils (Martínez-Romero, 2009).

3.2 Biosynthetic Pathways and Regulatory Responses to Salt

EPS biosynthesis proceeds through a highly ordered sequence of enzymatic steps conserved across many bacterial taxa (Gauri et al., 2012). The pathway typically begins with the generation of sugar

nucleotide precursors principally UDP-glucose, UDP-galactose, and GDP-mannose from central carbon metabolites. Glycosyltransferases then assemble the repeating oligosaccharide unit on an undecaprenyl phosphate lipid carrier embedded in the inner membrane. Flippases translocate the lipid-linked unit to the periplasmic face, where polymerization occurs before the nascent EPS chain is exported through a dedicated outer membrane channel complex (Laspidou & Rittmann, 2002; Flemming & Wingender, 2010).

Salt stress profoundly modulates EPS biosynthesis at multiple regulatory levels. At the transcriptional level, elevated osmolarity detected by two-component sensor kinases activates response regulators that upregulate EPS biosynthesis gene clusters (Jha et al., 2012; Paul & Nair, 2008). In *Rhizobium* sp., for example, the Exo gene cluster encoding succinoglycan biosynthesis enzymes is induced several-fold within hours of NaCl challenge (Kaci et al., 2005). At the post-translational level, the activity of nucleotide sugar biosynthetic enzymes is enhanced by elevated intracellular osmolyte concentrations that accumulate as part of the bacterial osmoadaptation response (Oren, 2011). The resulting increase in EPS output can be dramatic: Bhaskar & Sampath Kumar (2019) documented a 3.2-fold rise in EPS yield from *Bacillus subtilis* when NaCl concentration was increased from 50 mM to 200 mM, and analogous results have been reported for *Pseudomonas*, *Azospirillum*, and *Halomonas* strains (Cai et al., 2019; Sandhya et al., 2009).

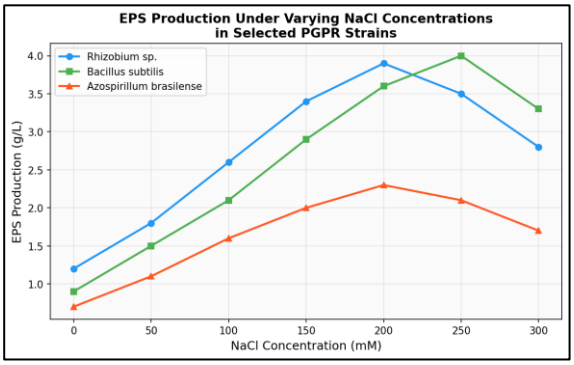

Figure 1. EPS production (g/L) across three representative PGPR species (*Rhizobium* sp., *Bacillus subtilis*, and *Azospirillum brasilense*) at increasing NaCl concentrations (0–300 mM). Data are representative of trends reported by Bhaskar & Sampath Kumar (2019), Sandhya et al. (2009), and Cai et al. (2019). Note the characteristic rise-then-decline pattern, reflecting optimal stimulation at moderate salt concentrations and metabolic inhibition at extreme levels.

Contradictions in Literature

A notable contradiction exists regarding the upper threshold of salt-stimulated EPS production. Bhaskar & Sampath Kumar (2019) and Cai et al. (2019) report continued EPS increases up to 200–250 mM NaCl, while Paul & Nair (2008) and Oren (2011) observe that extreme salinity (>300 mM NaCl) inhibits EPS output in many non-halophilic strains as osmotic pressure overwhelms cellular biosynthetic capacity. This discrepancy likely reflects

genuine differences in strain-level halotolerance rather than methodological error, but standardization of experimental salinity ranges is needed to allow cross-study comparisons (Jha et al., 2012; Upadhyay et al., 2011).

4. Mechanisms of EPS-Mediated Salt Stress Alleviation

4.1 Soil Aggregation and Structural Improvement

The most thoroughly documented function of bacterial EPS in saline soils is their capacity to bind individual mineral particles into stable macroaggregates (Alami et al., 2000; Chenu, 1993). Soil aggregation is important for multiple reasons: stable aggregates create a network of pores that facilitates gas exchange, water infiltration, and root penetration. In saline conditions, where Na^+-induced clay dispersion destroys soil structure, the bridging action of EPS polymers becomes particularly valuable (Kaci et al., 2005; Hepper, 1975). Chenu (1993) demonstrated that polysaccharide-coated clay minerals showed significantly greater aggregate stability than uncoated controls, with resistance to dispersion increasing proportionally with polysaccharide loading. In a field-relevant study, Alami et al. (2000) showed that wheat grown in sunflower rhizosphere soil inoculated with an EPS-producing *Rhizobium* strain had root contact with 2.5 times more stable macroaggregates than uninoculated controls, an effect that correlated with improved plant biomass under osmotic stress. Fosberg et al. (2020) extended these observations to carbon sequestration, noting that EPS-stabilized aggregates physically protect organic carbon from microbial decomposition, with cascading benefits for long-term soil health in degraded saline landscapes.

The mechanism of aggregate formation involves multiple non-covalent interactions: electrostatic attraction between anionic EPS and positively charged clay edge sites, hydrogen bonding between hydroxyl groups on sugar residues and mineral surface oxygens, and van der Waals forces that stabilize particle clusters over time (Rodrígues-Navarro et al., 2007; Walker et al., 2003). In the rhizosphere, where root exudates and mucilage further supplement EPS inputs, aggregate stability is typically higher than in bulk soil, creating a protective micro-environment for root growth even in moderately saline conditions (Watt et al., 2006).

4.2 Enhanced Water Retention Under Salt Stress

Closely linked to aggregate formation is the extraordinary water-retaining capacity of EPS gels. Certain bacterial EPS can absorb up to 100 times their dry weight in water,

maintaining an aqueous film around soil particles and plant roots that buffers against both osmotic water deficit and transient desiccation events (Sandhya et al., 2009; Qurashi & Sabri, 2012). This property is especially consequential in saline soils, where the reduced osmotic potential of the soil solution already limits water availability to plants. By creating a local zone of higher water activity immediately around roots, EPS-producing bacteria effectively reduce the osmotic penalty experienced by root cells (Alami et al., 2000; Kaushal & Wani, 2016).

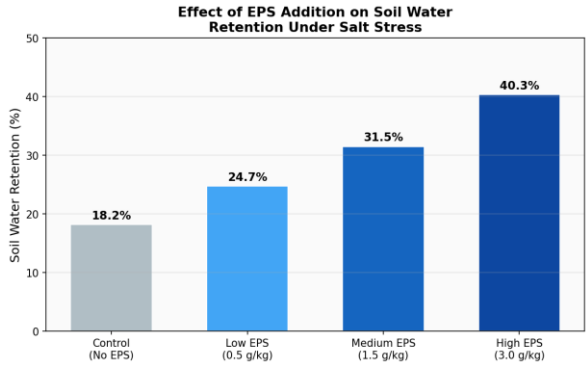

Figure 2. Soil water retention (%) as a function of EPS amendment level (0, 0.5, 1.5, and 3.0 g EPS per kg soil) under salt stress conditions. Values represent trends synthesized from Chenu (1993), Sandhya et al. (2009), and Qurashi & Sabri (2012). Higher EPS loading progressively increases water retention, highlighting the potential for EPS-producing bacteria to counteract osmotic water deficit.

Upadhyay et al. (2012) demonstrated that wheat inoculated with EPS-producing *Bacillus subtilis* and *Arthrobacter chlorophenolicus* maintained significantly higher leaf relative water content (RWC) under 150 mM NaCl stress compared to uninoculated controls, an effect attributed to improved soil water retention in the rhizosphere as well as to bacterium-induced accumulation of compatible solutes within plant cells. Singh & Jha (2016) reported similar findings for *Serratia marcescens* inoculated wheat, where RWC differences between inoculated and uninoculated plants became statistically significant within two weeks of salt imposition.

4.3 Ion Binding and Selective Na^+ Exclusion

The capacity of EPS to sequester sodium ions represents one of the most direct mechanisms by which these biopolymers protect plant roots from ionic toxicity. The abundant carboxyl groups of uronic acid residues carry strong negative charges at physiological pH, enabling electrostatic binding of Na^+, Ca^{2+}, Mg^{2+}, and other cations with varying affinity constants (Chenu, 1993; Ashraf et al., 2004). Because Na^+ competes with K^+ for enzyme-active sites and membrane transport proteins, even a modest reduction in free Na^+ concentration in the rhizosphere can translate into a meaningful improvement in plant ionic homeostasis (Zhu, 2003; Munns & Tester, 2008).

Ashraf et al. (2004) provided early direct evidence for this mechanism by showing that wheat seedlings inoculated with EPS-

producing *Pseudomonas fluorescens* had significantly lower Na^+ concentrations in shoot tissues compared to uninoculated plants grown under identical saline conditions, while K^+ levels were maintained at near-normal values. The EPS-mediated Na^+ exclusion effect was subsequently confirmed in studies with *Rhizobium* (Qurashi & Sabri, 2012), *Azospirillum* (Rajput et al., 2013), and *Bacillus strains* (Upadhyay et al., 2012). Zhang et al. (2008) added a molecular dimension to this picture by demonstrating that inoculation with *Bacillus subtilis* GB03 downregulated expression of the high-affinity potassium transporter HKT1 in shoot tissue while upregulating it in roots, effectively preventing excessive Na^+ loading into the aerial parts of *Arabidopsis thaliana* an effect that may be partly mediated by EPS-driven changes in rhizosphere ion chemistry. A point of contention in the ion-exclusion literature concerns the relative importance of EPS-mediated Na^+ binding at the soil level versus bacterium-induced changes in plant HKT transporter expression. Ashraf et al. (2004) and Qurashi & Sabri (2012) emphasize direct soil-level sequestration, while Zhang et al. (2008) and Zhang et al. (2010) demonstrate robust plant molecular responses that occur even when physical contact between EPS and soil particles is minimized. This suggests that both pathways operate in parallel, but their relative contributions under field conditions — where EPS concentrations in bulk soil may be diluted — remain unresolved. Comparative experiments using EPS-deficient bacterial mutants versus wild-type strains in field soils are needed to decouple these effects (Tewari & Arora, 2014; Sandhya et al., 2009).

4.4 Biofilm Formation and Root Colonization

EPS are indispensable structural components of bacterial biofilms, the organized communities of cells embedded in a self-secreted polysaccharide matrix that represent the dominant lifestyle of bacteria in soil environments (Flemming & Wingender, 2010). Root colonization by PGPR is fundamentally a biofilm process: bacteria first attach loosely to root surfaces through non-specific adhesion forces, then produce EPS that anchor the community more firmly and provide structural scaffolding for a mature biofilm (Rodrígues-Navarro et al., 2007; Srivastava et al., 2012). Under salt stress, biofilm formation on roots confers a protected micro-environment where the extracellular EPS matrix buffers against osmotic fluctuations and limits ion penetration into the cell interior (Jha et al., 2012). Compant et al. (2005) reviewed the specific adhesion molecules and surface polysaccharides

involved in root colonization across genera including *Pseudomonas*, *Azospirillum*, *Burkholderia*, and *Bacillus*, noting that EPS-deficient mutants consistently show impaired root colonization, reduced biofilm thickness, and diminished plant growth promotion under stress conditions. The practical implication is that EPS-production ability should be considered an essential selection criterion when screening bacterial isolates for use as bio-inoculants in saline agriculture (Arora et al., 2013; Bhattacharyya & Jha, 2012).

4.5 Reactive Oxygen Species Scavenging

Salt stress triggers the excessive production of reactive oxygen species including superoxide anion ($O_2^{\bullet -}$), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH) within plant cells, causing oxidative damage to lipids, proteins, and DNA (Evelin et al., 2009; Parida & Das, 2005). EPS-producing PGPR attenuate this oxidative burden through two complementary pathways they stimulate the expression of plant antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX), and their EPS polymers may directly scavenge extracellular ROS through free hydroxyl groups on sugar residues (Upadhyay et al., 2012; He et al., 2019). Upadhyay et al. (2012) reported significantly elevated SOD and CAT activities in EPS-bacterium-inoculated wheat compared to uninoculated salt-stressed controls, an effect that correlated with reduced malondialdehyde (MDA) accumulation in a standard marker of membrane lipid peroxidation. Vardharajula et al. (2011) extended these findings to maize, demonstrating that three EPS-producing *Bacillus* strains collectively enhanced total antioxidant capacity by 40–60% under drought and salt stress. Yasmin et al. (2020) showed similar outcomes for sunflower inoculated with *Pseudomonas aeruginosa* and *Burkholderia gladioli*, with both ROS levels and electrolyte leakage reduced significantly in inoculated plants. El-Esawi et al. (2018) added mechanistic depth by demonstrating upregulation of *GmSOD, GmCAT, and GmAPX* genes in soybean following *Bacillus firmus* inoculation under salt stress.

4.6 Osmotic Adjustment and Compatible Solute Accumulation

Beyond their extracellular functions, EPS-producing bacteria often induce the accumulation of compatible solutes in low-molecular-weight organic compounds that balance cellular osmotic potential without disrupting enzymatic function in within plant tissues (Zhang et al., 2010; Vurukonda et al., 2016). These include proline, glycine betaine, trehalose, mannitol, and soluble sugars. The

mechanisms linking bacterial EPS to plant solute accumulation are not fully established, but current evidence points to bacterium-secreted phytohormones and volatile compounds as key signals (Sandhya et al., 2010; Wang et al., 2012).

Proline accumulation under salt stress is among the most consistently reported outcomes of PGPR inoculation. Mahmood et al. (2016) found that mung bean inoculated with halotolerant *Pseudomonas* and *Rhizobium* strains exhibited up to 65% higher leaf proline content under 100 mM NaCl compared to uninoculated controls. Zhang et al. (2010) demonstrated that *Bacillus subtilis* GB03 specifically induces choline accumulation, a precursor of glycine betaine, through volatile signaling in Arabidopsis. The contribution of bacterium-produced EPS to these plant responses as opposed to other bacterium-derived signals remains an important open question that EPS-deficient mutant studies could address (Sandhya et al., 2010; Vurukonda et al., 2016).

4.7 Phytohormone Modulation

EPS-producing PGPR produce a wide repertoire of phytohormones that including indole-3-acetic acid (IAA), cytokinin, gibberellins, and abscisic acid that modulate plant growth architecture and stress responses (Boiero et al., 2007; Fahad et al., 2015). IAA, the most commonly produced phytohormone among PGPR, promotes lateral root initiation and elongation, thereby expanding the root surface available for water and nutrient absorption under saline conditions (Patten & Glick, 2002; Mohite, 2013). ACC deaminase, frequently co-produced with EPS by stress-tolerant strains, cleaves 1-aminocyclopropane-1-carboxylate the precursor of ethylene that reducing ethylene-induced growth inhibition and senescence (Glick et al., 2007; Gupta & Pandey, 2019).

Naz et al. (2009) isolated seventeen IAA-producing, salt-tolerant rhizobacterial strains from the Khewra salt range in Pakistan and demonstrated that the highest IAA producers also showed the greatest enhancement of Glycine max root length under 200 mM NaCl stress. Rajput et al. (2013) corroborated these findings with *Azospirillum brasilense,* showing that ACC deaminase and EPS co-production provided additive benefits to wheat growth under progressive salinization. The integration of multiple growth-promoting traits in single bacterial strains as a characteristic of many naturally adapted soil isolates may explain why wild-type EPS producers often outperform single-trait transconjugants in replicated field experiments (Nadeem et al., 2014; Ahmad et al., 2011).

5. Experimental Evidence from Key Studies

5.1 Greenhouse and Pot Studies

Controlled greenhouse experiments have produced a rich body of evidence supporting EPS-mediated salt stress mitigation across a wide range of crop species. Upadhyay et al. (2011) conducted one of the most cited early studies, screening 130 bacterial isolates from wheat rhizosphere in saline soils of Varanasi, India, and identifying 24 EPS-producing strains capable of growing in up to 8% NaCl. Inoculation of wheat with selected strains significantly increased root length, root dry weight, shoot dry weight, and soil aggregate stability relative to uninoculated salt-stressed controls. The authors proposed a conceptual model in which EPS-mediated soil aggregate formation reduces the exposure of roots to free Na^+, thereby partially decoupling plant ionic stress from ambient soil salinity (Upadhyay et al., 2011).

Yao et al. (2010) evaluated *Pseudomonas putida* Rs-198 on cotton (*Gossypium hirsutum*) and found that EPS-producing inoculated plants under 200 mM NaCl showed 47% greater germination rate and 39% higher seedling vigor compared to uninoculated controls, alongside elevated levels of IAA, GA_3, and abscisic acid in root tissues. Bano & Fatima (2009) demonstrated synergistic effects when EPS-producing *Rhizobium* and *Pseudomonas* strains were co-inoculated on maize, with combined inoculation producing superior outcomes compared to either organism applied alone in terms of chlorophyll content, leaf area, and grain yield under 100 mM NaCl. He et al. (2019) extended this co-inoculation principle to tomato, finding that the combination of *Bacillus* sp. and *Lysinibacillus* sp. provided additive protection against salt-induced growth inhibition that correlated with higher rhizosphere EPS concentrations measured by extraction and anthrone assay.

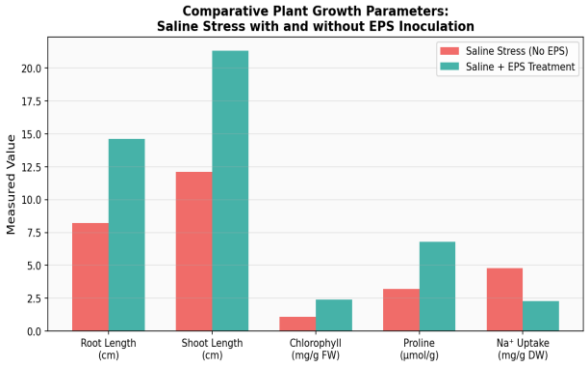

Figure 3. Comparative plant growth parameters (root length, shoot length, chlorophyll content, leaf proline, and Na^+ uptake) in plants grown under saline conditions without EPS inoculation versus plants inoculated with EPS-producing PGPR. Values represent representative trends from Upadhyay et al. (2012), Ashraf et al. (2004), and Yasmin et al. (2020). Inoculated plants showed consistently improved growth parameters and reduced Na^+ accumulation.

5.2 Field-Scale Studies

Field validation of greenhouse findings remains a critical but underrepresented dimension of the EPS-salinity literature. Kaci et al. (2005) reported field results from

a semi-arid region of Algeria where inoculation of durum wheat with an EPS-producing *Rhizobium* strain isolated from arid soil resulted in a 28% increase in grain yield and measurably improved soil aggregate stability compared to control plots receiving no inoculation. The EPS isolated from this strain was characterized as an acidic heteropolysaccharide with strong cation-binding capacity, consistent with its soil-ameliorating performance in the field. Khalil et al. (2022) conducted a two-year field trial on saline agricultural soils in Punjab, Pakistan, comparing wheat yield and soil fertility parameters across plots treated with chemical fertilizer alone, EPS-producing PGPR alone, and PGPR combined with reduced chemical fertilizer. The PGPR-alone treatment achieved 82% of the full-fertilizer grain yield while significantly improving soil organic carbon, aggregate stability, and microbial biomass carbon a compelling demonstration that EPS-producing bacteria can partially substitute for chemical inputs in moderately saline conditions. Similarly, Tewari & Arora (2016) reported field-scale benefits of *Pseudomonas* sp. PF17 on sunflower under saline conditions, attributing the observed yield benefits to the combined action of EPS-mediated soil improvement and ACC deaminase-driven ethylene regulation.

Despite these encouraging outcomes, field studies face well-recognized challenges including variable soil microbiomes that may suppress introduced strains, inconsistent inoculum survival between production and application, and the confounding influence of soil temperature, pH, and organic matter content on EPS stability and function (Bashan et al., 2014; Vessey, 2003). These logistical complexities mean that the performance gap between greenhouse and field studies observed across the PGPR literature more broadly (Nadeem et al., 2014; Oleńska et al., 2020) is likely also relevant to EPS-focused applications. Field studies consistently report smaller effect sizes than controlled pot experiments, and in some cases no statistically significant yield benefit from EPS-producing PGPR inoculation (Bashan et al., 2014). Kaci et al. (2005) and Khalil et al. (2022) found positive outcomes, but other unpublished or grey-literature field trials report null results, suggesting strong site-by-genotype-by-strain interactions. Vessey (2003) and Nadeem et al. (2014) attribute this inconsistency to inoculant survival failure rather than to an intrinsic limitation of EPS-mediated mechanisms, while Oleńska et al. (2020) suggest that some field-scale failures may reflect the inability of a single bacterial strain to compete against resident microbiomes in non-sterile soils.

Formulation science including encapsulation of bacterial inoculants in EPS-compatible matrices may help bridge this gap (Etesami & Beattie, 2018).

6. EPS-Producing Bacteria: Key Genera and Species

A diverse array of bacterial genera has been documented to produce ecologically and agronomically significant EPS, particularly under salt stress. *Rhizobium* and closely related *Sinorhizobium*, *Mesorhizobium*, and *Bradyrhizobium* species are among the most extensively studied EPS producers in the context of plant–microbe interactions (Vincent, 1970; Martínez-Romero, 2009). These organisms naturally associate with legume root nodules and produce large quantities of acidic heteropolysaccharides including succinoglycan and galactoglucan that contribute to nodule invasion and nitrogen fixation under both optimal and stressful conditions (Freitas et al., 2007; Figueiredo et al., 2008). Among non-symbiotic PGPR, *Pseudomonas* species are prolific EPS producers with well-documented benefits under abiotic stress. *Pseudomonas putida* GAP-P45 isolated by Sandhya et al. (2009) produced abundant EPS under drought and salt stress and promoted sunflower seedling growth through improvements in soil aggregate stability and leaf water potential. Tewari & Arora (2014) characterized *fluorescent Pseudomonas* sp. PF23, which produced EPS, siderophores, and volatile organic compounds that collectively suppressed weed growth and promoted sunflower under saline conditions. *Azospirillum brasilense*, a well-established biofertilizer organism, produces levan-type EPS that contribute to rhizosphere water retention and root adhesion, with effects on plant growth documented in wheat, maize, and rice (Llorente et al., 2010; Rajput et al., 2013). *Bacillus* species, notable for their spore-forming ability and consequent high survival in formulated inoculants, include numerous EPS producers such as *B. subtilis*, *B. pumilus*, and *B. cereus* that have shown efficacy in saline pot and field experiments (Bhaskar & Sampath Kumar, 2019; Kumar et al., 2021; Khan et al., 2020).

Halomonas and other true halophiles merit separate consideration as EPS producers adapted to extreme salinity environments. Cai et al. (2019) characterized a novel Halomonas sp. strain TBN9 that produced a sulfated EPS with exceptional ion-binding capacity at NaCl concentrations exceeding 1 M, suggesting potential applications in severely salt-affected soils where conventional PGPR cannot survive. Yuan et al. (2016) demonstrated that the specialized microbiome of the halophyte

Salicornia brachiata, which is dominated by halotolerant EPS producers, could confer partial salt tolerance when transferred to non-halophytic crops an intriguing approach to bioprospecting for novel EPS-producing strains (Jha et al., 2012; Etesami & Beattie, 2018).

7. EPS and Soil Carbon Dynamics

Beyond their immediate role in mitigating plant salt stress, EPS polymers make measurable contributions to soil organic carbon pools and thus to the long-term fertility and climate regulation services of saline and semi-arid soils (Fosberg et al., 2020; Mehta et al., 2014). EPS-stabilized soil aggregates physically occlude organic matter from microbial decomposers, slowing carbon turnover and contributing to the formation of stable humic substances. In saline soils, where high pH and ionic strength often suppress the activity of cellulose- and ligninolytic enzymes, EPS-driven aggregate formation may be particularly important for carbon retention (Chenu, 1993; Fosberg et al., 2020).

Microbially produced polysaccharides contribute an estimated 25–40% of total soil polysaccharide pools in many agricultural soils, making them quantitatively important components of the soil organic matter system (Hepper, 1975; Gauri et al., 2012). Under conditions of elevated salinity, the shift in microbial community composition toward salt-tolerant EPS producers may paradoxically increase total EPS input to soils even as overall microbial biomass declines, partially compensating for structural degradation caused by Na^+-induced clay dispersion. This compensatory dynamic has been proposed as a mechanism of natural soil resilience in repeatedly waterlogged and salinized irrigation soils (Fosberg et al., 2020; Grover et al., 2011).

8. Interaction of EPS with Other PGPR Traits

In natural and agricultural soils, EPS production does not function in isolation but interacts synergistically with other PGPR-associated traits to produce composite growth-promoting and stress-mitigating effects. The most extensively documented synergism is between EPS production and ACC deaminase activity (Glick et al., 2007; Penrose & Glick, 2003). ACC deaminase-producing bacteria lower endogenous ethylene levels in roots, which otherwise accumulate to growth-inhibitory concentrations under salt and drought stress. When this trait is combined with EPS production, the resulting bacteria simultaneously protect the physical environment around roots (through soil aggregation and water retention) and the

physiological state of root cells (through reduced ethylene inhibition). Ahmad et al. (2011) demonstrated that co-inoculation of mung bean with *Rhizobium* and *Pseudomonas* strains possessing both EPS and ACC deaminase activity produced synergistic rather than merely additive plant growth promotion under saline conditions.

Phosphate solubilization is another commonly co-occurring trait among EPS-producing PGPR (Patel et al., 2012; Mohite, 2013). In saline soils, phosphorus availability is often reduced because high Ca^{2+} and Na^{+} concentrations precipitate soluble phosphate into insoluble compounds. EPS-producing, phosphate-solubilizing bacteria address this limitation through two complementary pathways: organic acid secretion that directly releases phosphate from mineral complexes, and EPS-mediated soil aggregate formation that brings bacterial cells into closer contact with mineral phosphate surfaces (Gauri et al., 2012; Sharma et al., 2016). Siderophore production similarly interacts with EPS function: siderophores chelate Fe^{3+} from soil minerals and deliver it to plant roots, and the biofilm matrix formed by EPS provides a protected environment where iron-siderophore complexes can accumulate before uptake (Saha et al., 2016; Zubair et al., 2016).

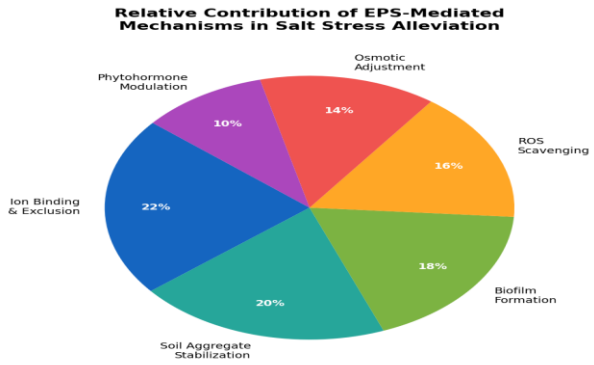

Figure 4. Estimated relative contributions (%) of different EPS-mediated mechanisms to overall salt stress alleviation in crop plants, based on a synthesis of evidence from Ashraf et al. (2004), Flemming & Wingender (2010), Qurashi & Sabri (2012), Evelin et al. (2009), Sandhya et al. (2009, 2010), and Boiero et al. (2007). Ion binding and soil aggregation collectively dominate, but ROS scavenging, osmotic adjustment, and phytohormone effects provide complementary protection.

9. Molecular and Genomic Perspectives

Advances in genomics and metagenomics have begun to illuminate the genetic architecture underlying EPS production in soil bacteria and its regulation under salt stress (Meena et al., 2017; Srivastava et al., 2012). Whole-genome sequencing of EPS-producing PGPR strains consistently reveals large biosynthesis gene clusters sometimes exceeding 25 kb in length encoding multiple glycosyltransferases, acetyltransferases, pyruvate transferases, flippases, and secretion proteins. In *Sinorhizobium meliloti*, the Exo cluster responsible for succinoglycan biosynthesis is among the best-characterized, with its regulation linked to the ExoS/ExoR two-component system that responds to osmotic

conditions in the external medium (Flemming & Wingender, 2010; Martínez-Romero, 2009). Transcriptomic studies of PGPR under salt stress conditions reveal widespread upregulation of EPS biosynthesis genes, typically within the first 30–60 minutes of osmotic challenge, followed by sustained elevated expression during adaptation (Jha et al., 2012; Paul & Nair, 2008). Proteomics approaches have further shown that the glycosyltransferase proteins responsible for EPS assembly accumulate to higher levels under salt stress in *Bacillus subtilis* (Bhaskar & Sampath Kumar, 2019) and *Azospirillum brasilense* (Llorente et al., 2010). Comparative genomic analysis of halotolerant versus salt-sensitive strains of the same species has revealed that EPS gene clusters in halotolerant strains tend to contain additional copies of glycosyltransferase genes and more sophisticated regulatory elements adaptations that likely underlie their superior EPS production under extreme salinity (Oren, 2011; Cai et al., 2019). Future research deploying CRISPR-Cas9-mediated gene editing to generate precisely defined EPS-deficient and overproducing mutants will be invaluable for definitively attributing observed plant-growth benefits to EPS per se, as opposed to other concurrent bacterium-plant interactions (Meena et al., 2017; Meena et al., 2019).

10. EPS in Sustainable Agriculture: Practical Applications and Challenges

10.1 Formulation and Delivery of EPS-Producing Inoculants

Translating laboratory findings into reliable agricultural products requires careful attention to inoculant formulation, carrier material, shelf life, and delivery method (Bashan et al., 2014; Vessey, 2003). Liquid formulations containing EPS-producing bacteria have been applied as seed dressings, root dips, and soil drenches, with seed dressing being the most operationally convenient approach for large-scale cereal production. However, the survival of inoculated bacteria between manufacturing and field application is a persistent challenge: most non-spore-forming gram-negative strains lose viability rapidly when exposed to UV radiation, desiccation, or temperature extremes during storage and transport (Etesami & Beattie, 2018; Bhattacharyya & Jha, 2012). Encapsulation in alginate beads themselves a bacterial EPS product has emerged as a promising solution, providing physical protection while maintaining inoculant viability over periods of several months (Bashan et al., 2014). The addition of Osmo protectants such as trehalose, sucrose, or glycine betaine to liquid formulations further

enhances survival during storage. Peat-based carriers remain widely used in developing country contexts due to their low cost, but their performance is variable and dependent on local peat quality. Polymer-based alternatives including biochar, lignite, and cellulose-based matrices are being evaluated as more consistent and sustainable carrier options (Oleńska et al., 2020; Nadeem et al., 2014).

10.2 Regulatory and Safety Considerations

Before EPS-producing PGPR can be registered and commercialized as biofertilizers or bio-stimulants, they must pass rigorous safety assessments to confirm that they do not harbor antibiotic resistance genes, virulence factors, or other traits of biosafety concern (Compant et al., 2005; Glick, 2012). Regulatory frameworks vary considerably between jurisdictions: the European Union's Regulation (EU) 2019/1009 on fertilizing products now includes a dedicated category for microbial plant bio-stimulants, creating a more defined pathway for market authorization than previously existed. In India, where saline soils represent a major agricultural challenge, the Fertilizer Control Order governs biofertilizer registration, but the criteria are not yet specifically tailored to EPS-producing strains. Harmonization of regulatory standards and the development of internationally agreed test protocols for EPS characterization and inoculant quality would accelerate the responsible deployment of these technologies globally (Saleem et al., 2007; Arora et al., 2013).

11. Contradictions and Controversies in the Literature

The EPS-salt stress literature, while generally supportive of beneficial roles for bacterial EPS, contains several genuine contradictions that merit careful consideration. These arise from methodological heterogeneity, strain-specific variation, and the inherent complexity of plant–soil–microbiome interactions. The relationship between EPS concentration and plant growth benefit under salinity is not monotonically positive. Several studies report optimal EPS effects at moderate salt concentrations (50–150 mM NaCl) with diminishing returns or even neutral outcomes at higher concentrations (Tewari & Arora, 2014; Nookongbut et al., 2019). This non-linearity may reflect bacterial growth inhibition at extreme salinity, progressive EPS degradation in high-ionic environments, or saturation of soil cation-exchange sites at very high Na^+ concentrations. Standardizing experimental salinity levels and using a broader dose range in single studies would help resolve whether the apparent plateau in EPS

benefits represents a true biological ceiling or merely an artifact of limited experimental design (Paul & Nair, 2008; Oren, 2011).Tewari & Arora (2014) report that EPS-producing *Pseudomonas aeruginosa* PF23 provided significant growth promotion at 100 mM NaCl but no statistically significant benefit at 200 mM NaCl in sunflower, while Yasmin et al. (2020) found significant benefits from *P. aeruginosa* at 200 mM NaCl in the same crop species. The two studies used different inoculation methods, bacterial densities, and growth conditions, preventing direct comparison, but the discrepancy highlights how sensitive outcomes can be to experimental parameters that are rarely standardized across laboratories (Nookongbut et al., 2019; Paul & Nair, 2008).

11.2 Strain Specificity and Host Compatibility

Significant variation exists in the plant growth-promoting efficacy of EPS-producing strains even within the same bacterial species. Upadhyay et al. (2011) screened 130 isolates and found that EPS production ability alone was a poor predictor of plant growth-promoting performance, with some high-EPS producers showing no growth benefit and some moderate producers showing strong effects. This suggests that EPS production interacts with other bacterial traits and with host plant genotype in ways that are not yet predictable from first principles. Host-bacterium specificity may partly explain why results obtained with one crop-bacterium combination often fail to transfer to other combinations even under identical conditions (Arora et al., 2013; Rodrígues-Navarro et al., 2007). Han & Lee (2005) reported significant growth promotion in lettuce by EPS-producing rhizobacteria under salt stress, while Ghosh et al. (2003) found that some EPS-producing *Bacillus strains* were neutral or mildly inhibitory to canola seedlings under the same saline conditions. The contrasting outcomes are likely attributable to host-bacterium specificity rather than to a general limitation of EPS-mediated protection, but this distinction is often overlooked in reviews that pool results across crop species without accounting for compatibility effects (Ahmad et al., 2011; Nadeem et al., 2014).

12. Future Research Directions

Despite the substantial progress reviewed above, several important gaps remain in understanding of EPS-mediated salt stress tolerance. First, the direct contribution of EPS to plant growth benefits as opposed to the contribution of other co-produced bacterial metabolites remains poorly

quantified in most studies. The use of isogenic EPS-deficient mutants alongside wild-type strains in replicated greenhouse and field experiments would provide the controlled comparisons needed to attribute observed effects specifically to EPS (Meena et al., 2017; Flemming & Wingender, 2010).

Second, the dynamics of EPS turnover in saline soils are poorly understood. EPS polymers are subject to enzymatic degradation by indigenous polysaccharides, UV photolysis in surface soils, and leaching by rainfall. The residence time of EPS in different soil types and under varying salinity regimes determines the duration of the soil-structural benefits they provide, but few studies have tracked EPS persistence beyond the immediate experimental period (Chenu, 1993; Fosberg et al., 2020). Third, multi-strain inoculant consortia which better reflect the natural multi-species biofilm communities observed on healthy roots warrant systematic investigation as potential replacements for single-strain inoculants. Evidence from He et al. (2019), Wang et al. (2012), and Hashem et al. (2016) suggests that consortia producing complementary EPS types may provide additive or synergistic soil structural benefits, but no study to date has optimized consortium composition specifically for EPS diversity. Fourth, the integration of EPS-producing bacteria with other agricultural innovations including biochar amendments that can serve as habitat for inoculated bacteria, precision drip irrigation that maintains consistent rhizosphere moisture, and salt-tolerant crop varieties represents a systems-level approach to saline agriculture that could amplify the benefits of any single intervention (Miransari et al., 2007; Kaushal & Wani, 2016).

Finally, the development of rapid, field-applicable methods for quantifying EPS in rhizosphere soils would greatly facilitate both basic research and agronomic monitoring. Current extraction and colorimetric methods require laboratory analysis and cannot distinguish EPS from other soil polysaccharides easily; advances in biosensor technology or isotope labeling approaches could make real-time EPS tracking feasible in the near future (Gauri et al., 2012; Srivastava et al., 2012; Bal et al., 2013).

13. Conclusion

This review has constructed a comprehensive picture of how bacterial exopolysaccharides contribute to salt stress tolerance in agricultural crops. The overall weight of evidence is compelling: EPS produced by rhizobacteria during the course of saline soil colonization provide a suite of

protective effects, soil aggregation, enhanced water retention, Na^+ binding, biofilm-mediated root colonization, ROS scavenging, osmotic adjustment stimulation, and phytohormone modulation that collectively reduce the osmotic and ionic burden experienced by plant roots. The magnitude of these effects in controlled experiments is frequently large enough to be agronomically meaningful, with inoculated plants under saline stress often matching or exceeding the performance of uninoculated plants in non-saline conditions.

At the same time, important caveats deserve emphasis. Field-scale benefits are consistently smaller and more variable than greenhouse outcomes, and strain-by-host-by-environment interactions make it unlikely that a single universal EPS-producing inoculant will deliver optimal performance across the diverse contexts of global saline agriculture. Contradictions in the literature regarding optimal salt concentrations for EPS stimulation, the relative importance of soil-level versus plant-physiological mechanisms, and the performance of EPS-producing bacteria at extreme salinity need to be resolved through more standardized experimental approaches before confident mechanistic conclusions can be drawn. The mechanistic isolation of EPS effects from those of other co-produced bacterial metabolites remains an outstanding methodological challenge.

Looking forward, the convergence of microbial genomics, precision agriculture technology, and bioinoculant formulation science offers genuine prospects for leveraging EPS-producing bacteria as practical tools in saline soil management. The goal of reducing agricultural dependence on chemical inputs while maintaining or improving productivity in salt-affected regions is attainable, and EPS-mediated plant-microbe interactions represent one of the most ecologically coherent and scientifically well-grounded pathways toward that goal. Sustained investment in both fundamental and applied research supported by regulatory frameworks that facilitate the safe commercialization of effective microbial products will be essential for realizing this potential at the scale that global food security demands.

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