

Review

Perspectives

Halophyte-associated salt-tolerant rhizobacteria: ecological adaptation, mechanistic pathways, and translational relevance for wheat salinity tolerance

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Running title: Halophyte- associated salt-tolerant rhizobacteria and wheat salinity tolerance

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Abstract

Background

Soil salinization is an expanding constraint to agricultural productivity worldwide, particularly in irrigated and arid regions and strongly limits wheat growth and yield. Although breeding and biotechnology have produced cultivars with improved ion-exclusion and tissue-level tolerance, these advances alone do not fully mitigate salinity-induced disruptions in rhizosphere processes and microbial activity. Salt-tolerant plant growth-promoting rhizobacteria (ST-PGPR) represent a complementary biological strategy and halophyte-derived strains are increasingly explored due to their pre-adaptation to saline environments. However, the influence of ecological origin on functional relevance and field performance remains poorly understood. This review synthesizes existing evidence on ST-PGPR effects in salinity-affected wheat with emphasis on inoculant origin.

Scope

We critically reviewed controlled-environment and field studies evaluating salt-tolerant PGPR in wheat under salinity stress. We compared the use of halophyte-derived versus non-halophyte-derived strains, summarized mechanistic contributions to nutrient acquisition, ion homeostasis, osmotic adjustment and oxidative stress mitigation and evaluated how these mechanisms translate into field-level yield responses. We also identified gaps in field validation and experimental design. Controlled studies consistently demonstrate physiological benefits of ST-PGPR, including improved germination, biomass, antioxidant capacity and stress resilience, although responses vary with wheat genotype and salinity intensity. Field evidence, however, remains limited, fragmented and mostly based on strains from non-saline soils, with inconsistent yield outcomes and few multi-season trials.

Conclusion

Halophyte-derived ST-PGPR represent a promising yet underexplored biological resource for saline agroecosystems. Translational success will require multi-site, multi-year field validation, assessment of persistence and ecologically-informed inoculant design to bridge controlled efficacy and reliable agronomic performance.

Keywords: Halophyte-associated rhizobacteria, ST-PGPR, wheat salinity tolerance, rhizosphere functioning, soil–plant–microbe interactions, microbial-assisted crop improvement.

INTRODUCTION

Soil salinization is a growing threat for the world's agriculture, especially in arid and semi-arid regions which largely depend on irrigation for crop production. Soil salinization significantly reduces agricultural productivity by impairing seed germination, plant growth, and yield, and is increasingly recognized as a major constraint to global food security. At the same time, naturally salt-adapted plants such as halophytes symbolize potential biological models for developing salinity-resilient agricultural strategies (Székely and Barta, 2025). Globally, more than 800 million hectares are affected, posing major risks to food security (Rengasamy, 2010). When soluble salts accumulate in the root zone of plants, they modify soil physicochemical properties, reduce nutrient availability and cause osmotic and ionic stresses, which harshly limit growth and yield (Munns and Tester, 2008; Rengasamy, 2010). Together, these plant- and microbe-level disruptions make salinity a highly complex stress which impairs plant performance in conjunction with disrupting the soils' biological activity. Salinity is also a strong ecological filter with the ability to restructure soil microbial communities, limiting diversity and shifting community composition towards salt-tolerant taxa along the salinity gradients (Zhang et al., 2019). Besides causing soil structural changes, elevated salinity also inhibits key microbial activity, organic matter degradation, nitrogen fixation, phosphorus uptake and sulfur metabolism, while selectively enriching a narrow set of stress-adapted pathways such as carbon fixation, denitrification and organic phosphorus dissolution (Li et al., 2024). Thus, salinity represents not only a physiological constraint for plants but also an impediment to rhizosphere activity, linking crop productivity losses with disrupted microbial ecosystem services. This dynamic implies that the origin of microbial inoculants may strongly influence their persistence, functional expression and activity in saline soils.

Rising temperatures, global warming and agricultural expansion into stress-prone lands are accelerating both the extent and severity of soil salinization. Munns and Gilliham (2015) emphasize that the severity of soil salinity is expected to worsen under the pressures of climate change and identify wheat as a salt-sensitive crop whose growth and yield declines in response to early osmotic stress and later, ionic toxicity. Complementing this, Munns et al. (2020) demonstrate that living in saline conditions requires major energy investments for ion exclusion, osmotic adjustments and photosynthesis maintenance. Increasing soil salinity progressively reduces plant growth and limits the energy available for grain production.

Wheat (*Triticum aestivum* L. and *T. durum* Desf.) is a moderately salt-tolerant crop when compared to other common cereals (Traye et al., 2025). Semi-dwarf bread-wheat yields begin to decline at an electric conductivity (EC) of $\sim 8.6 \text{ dS m}^{-1}$, whereas durum wheat's yield decreases above $\sim 5.9 \text{ dS m}^{-1}$ (Francois et al., 1986). Because EC is the standard measure of soil salinity, these values correspond closely to the agronomic thresholds used to classify saline soils: slight salinity (EC 2–4 dS m^{-1}), moderate salinity (4–8 dS m^{-1}), and strong salinity ($>8 \text{ dS m}^{-1}$) (Bosiacka et al., 2020). These thresholds are frequently exceeded in irrigated and salt-affected soils, limiting productivity in vulnerable regions. As one of the most widely cultivated staple crops worldwide, wheat underpins global food security by providing roughly one-fifth of humanity's caloric and protein intake, making its vulnerability to soil salinization a major agricultural and societal concern. Salinity triggers an initial osmotic water uptake-limitation and a simultaneous ionic imbalance caused in particular by Na^+ accumulation; these primary effects induce oxidative damages and metabolic disturbances which reshape cellular metabolism under stress (Zhu, 2016). Although breeding and biotechnology have produced cultivars with improved ion exclusion and tissue-level tolerance, the genetic benefits remain limited by the robust genotype–environment interactions and the polygenic structure of salinity tolerance (Roy et al., 2014).

Importantly, plant breeding alone is insufficient to counteract salinity-induced declines in soil microbial activity and nutrient cycling, highlighting the need for complementary rhizosphere-level strategies including the use of plant growth-promoting rhizobacteria (PGPR) (Shrivastava and Kumar, 2015). Plant growth-promoting rhizobacteria emerged as high-impact, effective biological agents for enhancing plant performance under abiotic stresses (Székely et al., 2022; Székely and Barta, 2022). They support plant growth through improving plant nutrient acquisition, modulating phytohormone dynamics and lowering the stress-induced ethylene production through ACC deaminase activity (Glick, 2014; Vessey, 2003). These functions are especially important under elevated salinity conditions, where nutrient imbalances, hormonal disruption and elevated ethylene production destabilize plant homeostasis. As a result, halophyte-derived salt-tolerant PGPR are increasingly explored due to their pre-adaptation to saline environments and their potential for more stable performance relative to strains isolated from non-saline soils (Egamberdieva et al., 2019). In this review, “halophyte-derived” refers specifically to bacterial strains isolated from the rhizosphere of halophytic plant species adapted to and growing in natural saline habitats. This definition excludes strains isolated solely from saline soils without a specific

halophyte host, as well as strains isolated from the rhizosphere of non-halophytic plants growing in salt-affected regions.

Under saline conditions, salt-tolerant PGPR (ST-PGPR) are especially valuable because they maintain their own growth and the expression of key plant-beneficial traits at high salinity, allowing them to function in environments where many conventional biofertilizers lose efficacy. Because halotolerant PGPR remain metabolically active under osmotic and ionic stress, they can continue to mobilize nutrients, modulate phytohormones, and attenuate plant ethylene levels even at high salinity (Etesami and Beattie, 2018). Controlled-environment studies consistently demonstrate that ST-PGPR improve wheat biomass and physiological performance under moderate to high salinity, emphasizing their functional relevance in saline agricultural systems (Orhan, 2016). However, most studies solely rely on strains isolated from non-saline agricultural soils and their ecological suitability for persistently saline environments thus remains uncertain. Microbial origin strongly affects inoculant performance, as plant-associated microbiomes are shaped by ecological filtering imposed by both the host's genotype as well as the environment, in particular, environmental stress (Berg et al., 2014). Strains isolated from halophytes are not only salt-tolerant but ecologically pre-adapted to function in high-salinity environments, shaped by long-term impacts of ionic and osmotic stress. Their chronic exposure often results in constitutive stress-responses allowing enhanced stability in trait expression under fluctuating conditions. Halophyte-derived bacteria therefore commonly show key salt-tolerance features, such as the enhanced production of osmoprotectants and exopolysaccharides, and specialized transport mechanisms, which support their sustained performance in saline soils (Egamberdieva et al., 2019). These traits suggest that halophyte-derived PGPR may exhibit greater functional stability and persistence in salt-affected wheat agroecosystems than strains originating from non-saline soils.

Despite these promising functional attributes, a persistent translation gap emerged: strong physiological benefits observed under controlled salinity conditions rarely translate into consistent yield gains in farmers' fields. To date, the field-level translation of the PGPR technology has proven inconsistent, with variable outcomes across different locations, seasons and wheat genotypes (Nadeem et al., 2013; Bashan et al., 2014; Sessitsch et al., 2019).

Despite the substantial advances, the ecological determinants of inoculant performance remain poorly understood. While numerous reviews have summarized PGPR-mediated salinity tolerance in crops, few have critically examined whether the ecological origin of inoculants

influences field performance, and none have systematically evaluated the lack of multi-season wheat field-validation of halophyte-derived strains as a limiting factor in agronomic deployment. This review aims to bridge this gap by synthesizing the current evidence on ST-PGPR effects on salinity-affected wheat, with specific emphasis on inoculant origin. We compare halophyte-derived and non-halophyte-derived strains, analyze their mechanistic roles in plant nutrient acquisition, ionic and osmotic regulation and oxidative stress mitigation, as well as critically evaluate how these mechanisms translate into field-level yield stability or yield gains. By explicitly identifying the ecological and agronomic barriers which constrain field reproducibility, we aim to define the research priorities necessary to move halophyte-derived ST-PGPR from proof-of-concept studies towards scalable applications in salt-affected wheat agroecosystems.

In addition to evaluating agronomic efficacy, we also propose a conceptual shift in how ST-PGPRs are conceptualized. Rather than viewing them primarily as yield-enhancing inputs, we transition to frame ST-PGPRs as stress-buffering symbionts whose principal advantage lies in their functional stability under chronic salinity. From this perspective, ecological origin represents a form of evolutionary pre-adaptation that may govern their resilience, persistence and consistency of beneficial traits in these microbial partners across fluctuating environments. This framing shifts focus beyond just trait enumeration, towards the benefits of ecological filtering and host–microbe co-adaptation as central determinants of translational success.

EVIDENCE FOR ST-PGPR–MEDIATED STRESS BUFFERING IN WHEAT UNDER CONTROLLED CONDITIONS

Controlled greenhouse and pot-based experiments consistently demonstrate that ST-PGPR can mitigate salinity stress in wheat. For example, inoculation with halotolerant *Pseudomonas chlororaphis* strains, in particular, strains producing phenazine, helped maintain shoot and root growth and biomass accumulation, improved relative water content and reduced the production of reactive oxygen species in leaves. Although phenazine primarily enhanced growth under non-saline conditions, all phenazine derivatives supported seedling resilience under salinity, with varietal differences in response magnitude (Yuan et al., 2020).

The application of biofertilizer consortia derived from halophyte rhizospheres (containing *Sporobolus montevidensis*, *Allenrolfea occidentalis*, *Atriplex portulacoides* and *Salicornia europaea*) resulted in modest but measurable improvements in durum wheat growth exposed to 85

mM NaCl, and simulated climate-change conditions of elevated CO₂ (700 ppm) and a 4°C increase in temperature (Redondo-Gómez et al., 2021). Biomass gains were moderate, indicating that halophyte-derived consortia function under salinity but deliver incremental rather than transformative improvements in controlled environments. These findings indicate that halophyte-derived consortia can be beneficial but are not uniformly effective across hosts or environments, underscoring the need for targeted strain selection and subsequent field validation.

In general, controlled studies report improvements in plant water status, antioxidant defense and biomass accumulation under saline conditions. However, the magnitude of these benefits widely varied across diverse wheat genotypes, bacterial functional traits and the degree of salinity. Hajiabadi et al. (2022) and Aizaz et al. (2023) conducted greenhouse experiments with the goal of evaluating the role of ST-PGPRs in improving wheat performance under salinity stress. Hajiabadi et al. (2022) explored the interactions between three PGPR strains (*Bacillus safensis*, *Bacillus pumilus* and *Zhihengliuella halotolerans*) and two wheat varieties, the salt-tolerant Narin and the salt-sensitive Qods variety. Their findings revealed, that ST-PGPR inoculation improved plant morphological traits, antioxidant activity and increased the proline, phenol and crude protein contents, in particular, in the salt-tolerant Narin variety. *B. safensis* increased grain dry weight by up to 50% in the Narin variety exposed to salt stress induced by 160 mM NaCl (Hajiabadi et al., 2022). The stronger response in the salt-tolerant genotype suggests that microbial benefits amplify existing host buffering capacity rather than fully compensating for severe sensitivity. Similarly, Aizaz et al. (2023) isolated 81 halotolerant bacterial strains from different environments (including plant tissues, rhizosphere soil, algae, etc.) and identified *Bacillus subtilis*, *Halospseudomonas pachastrellae*, and *Nitratioreductor aquimarinus* as the most effective strains in enhancing wheat growth under salt stress. These strains increased wheat shoot length by up to 24% and root length by up to 6%, together with seedling vigor and antioxidant enzyme activity with *Nitratioreductor aquimarinus* producing the largest gain in shoot length and *Halospseudomonas pachastrellae* showing the strongest enhancement of root growth (Aizaz et al., 2023). While very valuable, controlled-environment studies often focus on early vegetative traits, leaving long-term yield stability under chronic salinity largely untested. Taken together, these studies reinforce the physiological efficacy of ST-PGPR under controlled salinity while underscoring the importance of genotype-specific compatibility. In parallel, Alb daiwi et al. (2024) evaluated the efficacy of two halotolerant endophytic bacteria, *Pseudomonas jordanii* and *Oceanobacillus jordanicus* isolated

from the roots of field-grown durum wheat (a non-halophyte host), in two wheat genotypes differing in their salinity tolerance, Tamaroi, a salt-sensitive and Line 5004, a salt-tolerant genotype, under both greenhouse and field conditions. Under controlled salinity, the bacterial inoculation enhanced the physiological performance and biomass-related traits in both wheat genotypes, indicating an efficient mitigation of salinity-stress-associated responses. Interestingly, under field salinity conditions (soil EC 3.69 dS m⁻¹; irrigation water EC 7.57 dS m⁻¹), significant improvements in grain yield and yield-related parameters were primarily observed in the salt-sensitive Tamaroi variety, whereas the salt-tolerant Line 5004 only exhibited a limited, statistically non-significant response to the inoculation (Albdaiwi et al., 2024).

Overall, the controlled environment studies provide a strong mechanistic evidence to the findings that ST-PGPR treatments consistently enhance antioxidant defense capacity in wheat, improve the plants' osmotic adjustment capability and enhance biomass accumulation early in the plants' lifecycle. Yet the same studies also reveal limitations which constrain their predictive value for field conditions, predominantly associated with limitations of the testing methodologies, which tend to overestimate inoculant efficacy under homogenous controlled conditions relative to heterogeneous field conditions, underscoring the need for cautious interpretation and subsequent validation in realistic agroecosystem environments. A central reason for the potential overestimates is that greenhouse soil mixtures lack the dense, competitive resident microbiota found in field soils, thus missing the consideration of the ecological filtering pressures which may suppress inoculant establishment and trait expression. These considerations often frame a contrast with parallel field performance.

CONTRASTING EVIDENCE FOR ST-PGPR PERFORMANCE IN CONTROLLED CONDITIONS AND FIELD TRIAL

When compared to controlled environment studies, field trials yield more variable and context-dependent outcomes. Environmental heterogeneity, fluctuating salinity profiles and competitive exclusion by the resident microbiome frequently constrain inoculant establishment and functional persistence.

A key limitation of controlled-environment trials is the absence of long-term validation across diverse field environments characterized by fluctuating and continuously changing conditions. This lack of multi-season testing may constrain the establishment and persistence of

halophyte-derived bacterial inoculants under agronomically realistic conditions. Without multi-year field validation, it remains unclear whether the observed yield gains exceed natural seasonal variability or whether inoculant-induced effects are reproducible across years. As a result, an implementation gap persists between efficacy demonstrated under controlled conditions and reliability achieved in the field, underscoring the need for rigorous and ecologically grounded testing frameworks. These limitations frame the context in which existing field trials should be interpreted and help explain why controlled-environment success has not yet translated into predictable agronomic outcomes. Moreover, these structural constraints are further compounded by ecological processes operating at the soil–microbe–plant interface.

Ecological filtering, genotype dependence and greenhouse-driven overestimation collectively contribute to the gap between the outcomes observed under controlled conditions and those realized in the field. Responses of ST-PGPR vary strongly across wheat genotypes, with strain–host–environment interactions determining whether beneficial traits are expressed *in situ*. In contrast to field soils, greenhouse systems typically rely on homogenized substrates, reduced microbial competition and short experimental durations, factors which all systematically inflate the apparent inoculant efficacy. Together, these interacting constraints help explain why robust physiological improvements observed under controlled salinity often fail to translate into stable yield gains under agronomically realistic conditions (Fig. 1).

FIELD-BASED EVIDENCE FOR ST-PGPR PERFORMANCE IN WHEAT

Field studies show that ST-PGPR may enhance wheat yield under natural saline conditions. However, the overall evidence-base remains fragmented and heavily weighted towards strains isolated from non-halophytic environments, limiting robust conclusions regarding the agronomic value of halophyte-derived inoculants. For example, inoculation with *Pseudomonas putida*, *P. fluorescens*, *Enterobacter cloacae* and *Serratia ficaria* increased grain yield by up to 31% compared to the uninoculated controls under field conditions (Table 1.). These gains were accompanied by higher 1,000-grain weights (an up to 72% increase), higher grain number per spike (an up to 68% increase), and enhanced nutrient uptake, in particular, N, P, and K (Nadeem et al., 2013). Rajput et al. (2013) conducted a two-season field trial at a single saline site, demonstrating that the salt-tolerant wheat rhizobacterium *Planococcus rifietoensis* SAL15 substantially increased plant growth, biomass and grain yield under moderate salinity (Rajput et al., 2013) (Table 1).

Although meaningful from an agronomic perspective, these strains originate from non-saline agricultural soils rather than naturally saline ecosystems, providing limited insight into the role of ecological pre-adaptation. Co-inoculation of wheat with *Trichoderma harzianum* and *Bacillus amyloliquefaciens* enhanced grain yield under saline-sodic soil conditions (Table 1.), accompanied by improvements in spike traits, seed weight and physiological resilience (Singh et al., 2021). The most extensive dataset to date is provided by Diaz et al. (2022), with 25 field assays conducted across three sites and seven growing seasons in the Argentine Pampas, encompassing multiple wheat cultivars, and soil types, all of which demonstrated a consistent average grain-yield increase of 8% following seed inoculation with *Pseudomonas pergaminensis* (Diaz et al., 2022). Marghoob et al. (2023) demonstrated that halotolerant microbial consortia, with the bacterial strains *Erwinia rhapontici*, *Pantoea agglomerans* and *Pantoea* spp. also increased wheat grain yield under saline field conditions (Table 1). Field trials over one growing season at each of three salt-affected sites, evidenced that bio-priming with bacterial consortia enhances spike traits, grain number, 1000-grain weight and total plot yield. Notably, the bacterial consortium itself showed better performance than under either the fungal consortium or the reduced-fertilizer controls across all saline conditions tested. This study reported increased shoot lengths, dry weight and total plot yield for inoculated wheat (Marghoob et al., 2023). These findings suggest that consortia may buffer environmental variability more effectively than single strains, despite their non-halophytic origin. In contrast to these single-season evaluations, Alb Daiwi et al. (2024) conducted a multi-season and multi-site field trial, reporting that inoculation with *Pseudomonas jordanii* and *Oceanobacillus jordanicus* improved grain yields and agronomic traits in the salt-sensitive Tamaroi genotype, whereas the salt-tolerant Line 5004 displayed limited benefits from the inoculant treatment (Alb Daiwi et al., 2024).

Across all studies, the methodological limitations, including single-season designs and limited replicates, complicate cross-site comparisons and obscure the real benefits of inoculants and their field performance. From among the available studies, solely Rajput et al. (2013), Díaz et al. (2022) and Alb Daiwi et al. (2024) conducted multi-season field trials, whereas all other evaluations were limited to a single season, therefore providing only limited datasets without informing about the inoculants' benefits and field performance in respect of year-to-year stability, especially, under fluctuating salinity conditions. Remarkably, none of the multi-season studies employed

halophyte-derived strains, leaving the long-term agronomic potential of ecologically salinity pre-adapted inoculants untested.

Overall, the strength of current evidence lies in the documentation of the physiological and molecular effects of ST-PGPR under controlled salinity, whereas reproducibility, agronomic robustness and multi-environment validation remain solely marginally explored. It is also a notable finding that microbial consortia often show greater reproducibility than single-strain inoculants, likely to be attributable to their functional redundancy and potential complementary stress-response trait (Lin et al., 2023; Liu et al., 2023) . These advantages are still unexplored across diverse stress environments. The above imbalances highlight a need for additional rigorous experimental design, detailed surveys of soil and environmental parameters and standardized inoculant formulations in future studies exploring the beneficial effects of ST-PGPR on wheat salinity tolerance. The evidence most closely simulating field-relevant conditions derives from greenhouse and pot-based trials using halophyte-associated strains (Redondo-Gómez et al., 2021) and from true field-trials employing halotolerant endophytic strains originally isolated from the root tissues of field-grown durum wheat (Albdaiwi et al., 2024). As these organisms are adapted to saline habitats, the halophyte-derived PGPR represent a yet underexplored, highly promising pool of potential soil supplements for enhancing cereal health and productivity, thereby also enhancing the agricultural production of grain crops in salt-affected soils. Taken together, these constraints reveal a persistent field-translation barrier: despite clear physiological benefits under controlled salinity, ST-PGPR rarely deliver reproducible yield gains under field conditions, as most inoculants fail to persist, compete or maintain their functional activity within complex, salinity-filtered soil microbiomes.

To move beyond proof-of-concept, it is fundamental to perform multi-site and multi-year wheat field trials using well-characterized halophyte-derived inoculants. Ideally, the selected inoculants are expected to be tested on diverse wheat genotypes, under well-characterized soil salinity conditions, with direct assessment of the persistence of the inoculants as well as their beneficial effects on wheat growth, development and yield. This kind of detail-oriented validation is fundamental for bridging the gap between the efficacy of strains detected in controlled-environments and reliable performance under typical agroecosystem conditions in the field in applied crop production practices. Equally important is the optimization of ST-PGPR strain- or consortia-delivery systems which enhance their establishment under competitive field conditions. Addressing these ecological and methodological limitations is essential for advancing

halophyte-derived ST-PGPRs from promising experimental to reliable tools for wheat production in saline soils.

MECHANISTIC PATHWAYS UNDERLYING PGPR-MEDIATED SALT TOLERANCE

To better understand the variability of ST-PGPR-induced responses across varying environments, is necessary to examine the mechanistic foundations of ST-PGPR-mediated stress tolerance. Salt-tolerant PGPR (ST-PGPR) enhance wheat resilience through interconnected mechanisms that converge towards improved physiological performance and agronomic stability (Fig. 2). Rather than acting through isolated traits, these bacteria simultaneously improve nutrient mobilization, ion homeostasis, osmotic adjustment, and antioxidant regulation in plants, through an integrated buffering network that stabilizes plant function under salinity stress. Across these pathways, the halophyte-derived PGPR often retain functional activity at salinity levels that otherwise suppress non-halophytic strains, supporting the hypothesis that ecological origin enhances the stability and field persistence of their stress-mitigating capacity.

ST-PGPR impacts on plant nutrient acquisition

Salinity reduces nutrient bioavailability and root uptake efficiency, in particular for phosphorus (P) (Loudari et al., 2022), nitrogen (N) (Ullrich, 2004) and iron (Fe) (Ghassemi-Golezani et al., 2024). ST-PGPRs may partially compensate for this through phosphate solubilization, biological nitrogen fixation and siderophore production (Redondo-Gómez et al., 2021; Ramasamy and Mahawar, 2023). Halotolerant bacterial isolates obtained from saline environments, of the genera *Bacillus*, *Oceanobacillus* and *Halomonas*, exhibited organic acid-mediated phosphate solubilization, improved germination and seedling root growth under high salinity conditions (Albdaiwi et al., 2019). Similarly, *Oceanobacillus picturae*, isolated from the mangrove species *Avicennia marina*, mobilized up to 97% of the rock-phosphate under saline conditions by organic acid secretion and phosphatase activity (El-Tarabily and Youssef, 2010).

Several halotolerant nitrogen-fixing strains also enhanced wheat growth under saline conditions. Inoculation with halophilic and halotolerant strains improved root and shoot length, and fresh weight of wheat exposed to 200 mM NaCl (Orhan, 2016). Rhizospheric and endophytic isolates from saline soils near the Dead Sea, including *Halomonas campaniensis*, *Gracilibacillus timonensis*, *B. subtilis* and *B. licheniformis*, displayed nitrogen-fixing capacity and significantly

enhanced the germination and root growth in wheat seedlings under high salinity (Albdaiwi et al., 2019). Iron limitation in saline and calcareous soils can be alleviated through siderophore production by bacterial strains. Halotolerant strains isolated from the rhizosphere of wheat growing under saline conditions, including *Halomonas campaniensis*, *Gracilibacillus timonensis*, *B. subtilis*, *B. licheniformis* and *Azospirillum lipoferum*, produced siderophores and improved the germination and root growth of seedlings under saline conditions (Albdaiwi et al., 2019). Siderophore production by *B. aryabhattai* persisted even under 200 mM NaCl concentrations, although at reduced levels, when compared to control, non-saline conditions and continued to mobilize Fe even under a combination of saline and Fe-depleted conditions (Sultana et al., 2021). Collectively, these findings suggest that ST-PGPR buffer against nutrient constraints imposed by salinity by sustaining P, N and Fe availability, supporting early growth and metabolic stability in wheat. The benefits observed with halophyte-derived strains suggest that nutrient-mobilizing functions such as P solubilization, N fixation and siderophore production can remain active under saline conditions, reflecting the ecological adaptation of these microbes to saline habitats (Egamberdieva et al., 2019; Redondo-Gómez et al., 2021).

ST-PGPR effects on ion homeostasis and osmotic regulation

In plants, salinity disrupts the ionic homeostasis by enhancing Na^+ accumulation and impairing K^+ retention. ST-PGPR contribute to maintaining the K^+/Na^+ balance and enhancing the osmotic adjustment efficiency in wheat. Halophyte-derived and halotolerant PGPR reduce Na^+ accumulation, enhance K^+ uptake and improve the K^+/Na^+ ratio through mechanisms related to exopolysaccharide (EPS) production, the stimulation of ion transport systems and the stimulation of root development (Etesami and Beattie, 2018). Inoculation with *B. altitudinis* reduced Na^+ accumulation and increased K^+ , P and Ca^{2+} uptake in salt-stressed wheat, through the upregulation of the genes encoding for the plasma membrane H^+ -ATPase and via biofilm formation (Yue et al., 2022). Similarly, *Pseudomonas jordanii* and *Oceanobacillus jordanicus* influenced Na^+ and Ca^{2+} uptake, however, in a genotype-dependent manner, with the strongest detected effects in the salt-sensitive durum wheat genotypes (Albdaiwi et al., 2024).

Plant intrinsic mechanisms also contribute to maintaining osmotic balance. Durum wheat achieves osmotic balance through the coordinated accumulation of K^+ , Na^+ , and Cl^- , whereas bread-wheat synthesizes additional organic osmolytes (Cuin et al., 2009). Salinity tolerance further

depends on cytosolic Na^+ exclusion mediated by Salt Overly Sensitive 1 (SOS1) - like Na^+/H^+ antiporters and vacuolar Na^+/H^+ exchanger 1 (NHX1) transporters (Cuin et al., 2011).

Microbial EPS production complements plant responses to salinity. EPS-producing halophilic strains such as *B. subtilis* and *Marinobacter lipolyticus* reduced Na^+ uptake and enhanced K^+/Na^+ and $\text{Ca}^{2+}/\text{Na}^+$ ratios, increasing biomass at an EC of 16 dS m^{-1} (Atouei et al., 2019). In addition, inoculation with halotolerant strains enhanced the accumulation of the osmotically active small amino acid proline (Pro), as part of the plant's osmotic adjustments under high salinity (Amna et al., 2019). Genotype-dependent increases in soluble sugars and enhanced antioxidant activity were also reported in salt-tolerant wheat cultivars (Hussain et al., 2022). These findings suggest that ST-PGPR contribute to maintaining ion homeostasis and osmotic stability in wheat under saline conditions, through complementary microbial and plant transport processes, with responses shaped by the host plant's genotype. Since halophyte-derived PGPR evolve under chronic ionic imbalance conditions, their EPS production, ion-transport stimulation, and osmolyte production-related traits exhibit greater stability, or, inducibility in heavily saline environments, providing a plausible mechanistic explanation for their enhanced persistence and functional reliability in saline wheat rhizospheres.

Oxidative stress mitigation and growth responses to ST-PGPR in wheat

Salt stress-induced increases in reactive oxygen species (ROS) production induce the peroxidation of membrane lipids, damage proteins and disrupt cellular metabolism (Shabala et al., 2012). Salt-tolerant wheat cultivars exhibited elevated antioxidant enzyme activities (for example, superoxide dismutase (SOD); catalase (CAT); peroxidase, (POD); and ascorbate peroxidase (APX) activities), accompanied by reduced malondialdehyde (MDA), an indicator of lipid peroxidation and oxidative membrane damages) levels and increased proline and soluble sugar concentrations, upon exposure to 150 mM NaCl (Hussain et al., 2022). ST-PGPR amplified plant antioxidant defense capacities and stimulated osmolyte accumulation under saline conditions, in controlled environments (Etesami and Beattie, 2018).

Halotolerant *Bacillus* strains characterized by EPS production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, auxin synthesis, phosphate and zinc (Zn) solubilizing capacity, significantly improved the germination percentage, root and shoot length, seedling biomass, the tissue-concentration of photosynthetic pigments, and proline accumulation under

saline conditions characterized by ECs of 4–16 dS m⁻¹ (Amna et al., 2019). Similarly, inoculation with halotolerant strains increased the root and shoot length, as well as the total fresh weight of wheat seedlings exposed to 200 mM NaCl (Orhan, 2016), while *B. safensis* and *Zhihengliuella halotolerans* increased the dry weight, chlorophyll content, and grain dry weight in wheat exposed to 160 mM NaCl (Hajiabadi et al., 2022). Halophyte-derived consortia containing *B. methylotrophicus*, *B. aryabhattai* and *B. licheniformis* increased wheat above-ground biomass at 85 mM NaCl under elevated CO₂ (700 ppm) and temperature (at +4 °C higher than non-inoculated control plants) (Redondo-Gómez et al., 2021). These findings suggest that ST-PGPR, by modulating the crop's antioxidant system and reinforcing sustained osmotic balance, contribute to quantifiable agronomic benefits. Nevertheless, the specific extent of the conferred benefits remains contingent on bacterial persistence, host compatibility, and ecological filtering.

Halophyte-derived strains, in particular, exhibit robust modulation of antioxidant systems even at high salinity, suggesting that prolonged exposure to oxidative stress in their native habitats may enhance the stability of these protective mechanisms when introduced into crop systems.

CONCLUSION

Translating ST-PGPR efficacy from controlled systems to field applications presents several challenges and future research directions. Despite robust evidence from controlled experiments, the field translation of the benefits of ST-PGPR applications remains inconsistent and often site- and cultivar-specific. When applied under field conditions, inoculants are introduced into pre-assembled microbial communities shaped by long-term environmental filtering and naturally occurring environmental disturbances. The crop yield-improving ability of ST-PGPR under natural saline conditions is influenced by environmental heterogeneity, soil physicochemical constraints, and competition with native microbiomes, indicating that field performance is highly dependent on whether the introduced strains are able to establish long-term persistence in the existing soil–plant–microbiome systems, not on whether they induce benefits isolation. Collectively, these multi-scale limitations cause an environmental reliability gap that constrains the adoption of microbial biofertilizers in salt-affected wheat systems.

Advances in the formulation and delivery of inoculants, such as seed coating, bio-priming, and the use of protective carriers, are expected to enhance inoculant survival and improve the efficiency of rhizosphere colonization. Collectively, these approaches aim to bridge the gap

between proven laboratory potential and field performance, by prioritizing bacterial establishment in agroecosystems and long-term functionality within complex soil–plant–microbiome systems. The lack of consistent, predictable yield benefits delivered by PGPRs under field conditions enhances the need for ecologically-informed inoculant selection, improved formulation technologies, and the systematic evaluation of persistence and functional stability across various environments.

Advancing the applications of ST-PGPR from proof-of-concept to agricultural practice will require integrating field-relevant ecological complexity into inoculant development. Multi-season, multi-site, and multi-environment field trials are essential to determine whether yield gains exceed natural environmental variability and to identify the conditions under which the halophyte-derived strains outperform conventional inoculants. The direct assessment of inoculant persistence by tracking colonization, survival, and functional activity *in situ*, to clarify whether field responses reflect sustained microbial action or solely transient effects, is fundamental. Future work is also expected to prioritize ecological matching, aligning inoculant origins with wheat genotype, soil salinity profiles, and local microbial communities. Emerging approaches in soil microbiome engineering, including microbiome-informed inoculant design, synthetic microbial communities, and targeted microbiome steering, offer promising avenues to improve inoculant persistence and functional reliability under elevated field salinity. Microbial consortia designed for functional redundancy and complementary stress-response traits may offer greater resilience than single strains and warrant systematic evaluation under heterogeneous field conditions. Standardized reporting of soil salinity, environmental parameters, and inoculant formulation is likely to further improve cross-study comparability and enable the robust synthesis of data across studies.

Ultimately, translational success depends on ecological compatibility and persistence, not trait occurrence alone. Recognizing ST-PGPR as stress-buffering symbionts shaped by evolutionary history, and evaluating them within the ecological constraints of saline soils will be key to developing reliable microbial strategies for sustaining wheat production in salt-affected landscapes. Harnessing environmentally adapted microbial partners may ultimately contribute to more resilient wheat production systems in an era of expanding salinity and climatic uncertainty.

When considered at the scale of global wheat production, even modest yield stabilization under salinity assumes substantial significance. Preliminary projections from our ongoing analysis (Barta et al. 2026 personal communication), grounded in the range of responses reported in

published field trials (Table 1), indicate that conservative ST-PGPR–associated gains of 2–5% under moderately saline conditions could translate into tens of millions of additional tons of wheat annually across salt-affected production regions. In more responsive genotype–environment contexts, improvements in the range of 5–8% would represent even larger cumulative contributions to global food supply. In a crop exceeding 750 million tons of annual production, incremental yet reproducible gains in stress-buffered yield are not trivial—they represent meaningful leverage against expanding soil salinization and climatic instability. Realizing this potential, however, will ultimately depend on rigorous multi-season field validation and ecologically grounded deployment strategies capable of translating controlled-condition efficacy into durable agronomic outcomes.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

G.S. and C.B. conceived the review topic and structure. G.S., C.B., B.K., S.S. and P.A.S. conducted the literature search and analysis. G.S. and C.B. wrote the manuscript. All authors contributed to revisions and approved the final version.

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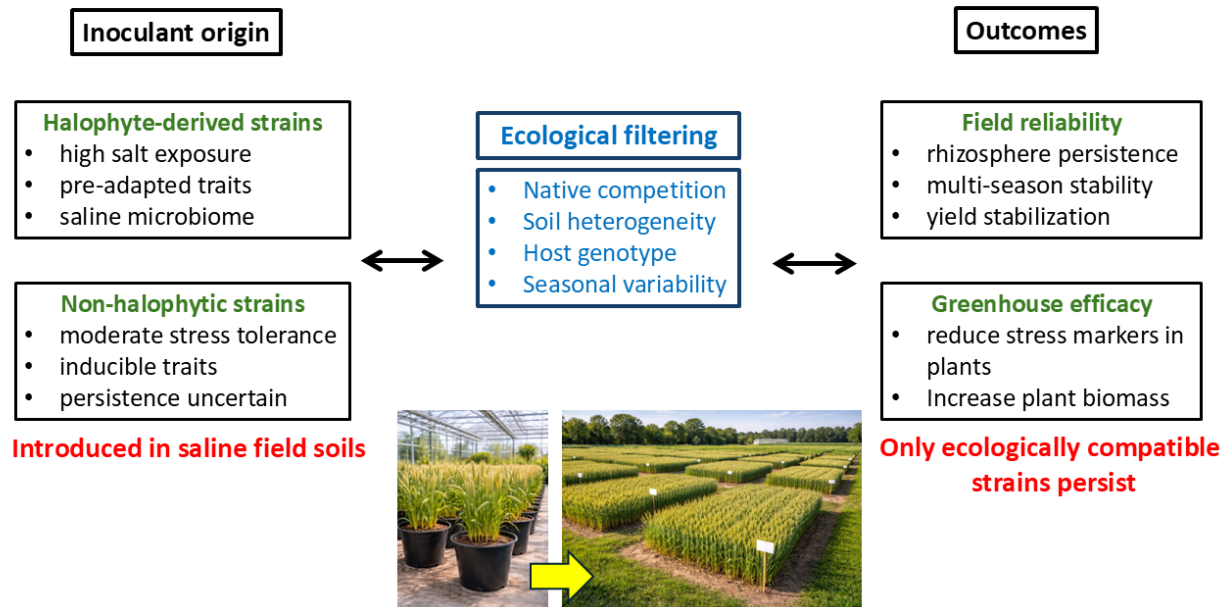
1 TABLES

2 **Table 1.** Currently available published field studies evaluating ST-PGPR efficacy in enhancing wheat yield under salinity stress

No.	Strain(s)	Strain isolation source	Field location (Country)	Nr. of sites (s), and nr. of seasons (S)	Soil salinity (ds m ⁻¹)	Wheat species	Grain yield increase (%)	Reference
1.	<i>Pseudomonas putida</i> , <i>P. fluorescens</i> , <i>Enterobacter cloacae</i> , <i>Serratia ficaria</i>	Not specified	Pakistan	s: 2, S: 1	11.8; 14.2	<i>Triticum aestivum</i>	24-31	(Nadeem et al., 2013)
2.	<i>Planococcus rifietoensis</i> SAL15	Wheat rhizosphere	Pakistan	s: 1, S: 2	7.63	<i>Triticum aestivum</i>	38–113	(Rajput et al., 2013)
3.	<i>Bacillus amyloliquefaciens</i> B16, <i>Trichoderma harzianum</i> UBSTH501	Agricultural soil (non-halophytic)	India	s: 1, S: 1	1.8	<i>Triticum aestivum</i>	19	(Singh et al., 2021)
4.	<i>Pseudomonas pergaminensis</i> 1008T	Wheat rhizosphere	Argentina	s: 3, S: 7	Not specified	<i>Triticum aestivum</i>	8	(Díaz et al., 2022)
5.	<i>Erwinia rhapontici</i> UM16, <i>Pantoea</i>	Saline soil	Pakistan	s: 3, S: 2	6.31; 7.18; 7.92	<i>Triticum aestivum</i>	4-22	(Marghoob et al., 2023)

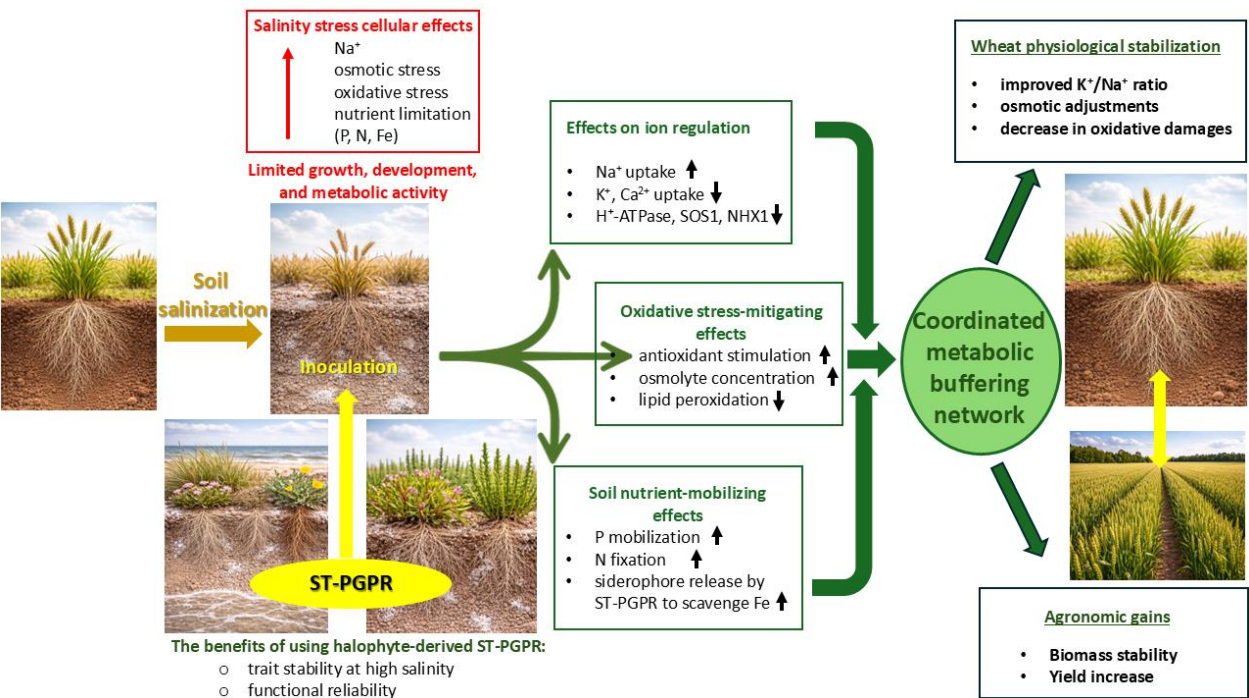
	<i>agglomerans</i> UM58, <i>Pantoea</i> sp. UM83			(single site / season)				
6.	<i>Pseudomonas</i> <i>jordanii</i> G34, <i>Oceanobacillus</i> <i>jordanicus</i> GSFE11, <i>Stenotrophomonas</i> <i>rhizophila</i>	Root tissue of Durum wheat	Jordan	s: 2, S: 2	3.69	<i>Triticum</i> <i>turgidum</i> ssp. <i>durum</i>	66-82	(Albdaiwi et al., 2024)

1 **FIGURES**



2 **Translational success depends on ecological compatibility and persistence, not only on trait occurrence.**

3 **Fig. 1.** PGPR ecological origin – persistence – field reliability model: the influence of ecological
4 origin on inoculant persistence and beneficial impacts on improving plant salt tolerance



- 1 **Fig. 2.** Mechanistic framework linking ST-PGPR functions to wheat stress buffering and
- 2 agronomic resilience under salinity.