ID: 869

Rhizobacterial Strategies for Abiotic Stress Mitigation: From Molecular Mechanisms to Precision Microbiome Management

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Abstract

Rice (*Oryza sativa* L.) is the primary staple crop for more than 3.5 billion people in tropical and subtropical regions, yet salt and drought stresses are increasingly constraining its productivity under accelerating climate change. Plant growth-promoting rhizobacteria (PGPR) offer a sustainable biological strategy to enhance rice resilience, but a quantitative synthesis of their effectiveness under tropical conditions has been lacking. This systematic review and meta-analysis quantified the overall effectiveness of PGPR inoculation in alleviating salt and drought stress in rice cultivated under tropical climates and identified key moderating factors. A systematic search of PubMed, Scopus, Web of Science, and Google Scholar identified 1,284 records, from which 50 peer-reviewed studies (published 2004–2023) meeting strict eligibility criteria were included in the quantitative synthesis. Effect sizes were calculated as Hedges' g under a random-effects model. Heterogeneity was assessed using the I^2 statistic, and subgroup analyses examined moderating effects of PGPR genus, stress type, experimental design, rice variety, and inoculation method. Publication bias was evaluated using Egger's test and funnel plot symmetry. PGPR inoculation produced significant positive effects across all measured outcomes. The pooled effect size for grain yield was Hedges' $g = 0.82$ (95% CI: 0.71–0.93; $p < 0.001$), representing a mean yield increase of approximately 32–48% under stress conditions. Combined stress treatments (salt + drought) showed the greatest improvements ($g = 1.08$). Mixed PGPR consortia outperformed single-strain inoculants. Field studies exhibited smaller but still ecologically meaningful effect sizes compared to greenhouse experiments. Heterogeneity was moderate to high ($I^2 = 57.9$–81.2%), partly explained by moderator variables. PGPR represents a scientifically robust and practically viable intervention for enhancing rice productivity under salt and drought stress in tropical environments. Future research should prioritize multi-strain consortium optimization, field validation across diverse tropical agro-ecosystems, and molecular characterization of key stress-tolerance pathways.

Keywords: *PGPR; salt stress; drought stress; Oryza sativa; rhizosphere*

Introduction

Rice (*Oryza sativa* L.) constitutes the dietary foundation for approximately 3.5 billion people worldwide, supplying more than 20% of daily caloric intake in Asia, sub-Saharan Africa, and Latin America (FAOSTAT, 2023). The overwhelming majority of global rice production is concentrated in tropical and subtropical regions where soil and climatic variability impose severe constraints on crop performance (IPCC, 2022). Among abiotic stresses, salinity and drought are universally recognized as the two most yield-declining factors in tropical rice ecosystems, collectively responsible for annual production losses estimated at USD 12–27 billion (Mahajan & Tuteja, 2005; Fahad et al., 2015).

Soil salinity, defined by electrical conductivity (EC) exceeding 4 dS m^{-1}, affects an estimated 800 million hectares globally, with approximately 20% of all irrigated agricultural land being salt affected (Porcel et al., 2012). In tropical deltas and coastal agro-ecosystems, including the Bengal Delta, Mekong Delta, and Chao Phraya plain secondary salinization is accelerating due to sea-level rise, storm surge intrusion, and unsustainable irrigation practices (Etesami & Beattie, 2018). Simultaneously, climate projections under the IPCC AR6 scenarios indicate that tropical regions will experience more frequent and intense drought episodes, with a 20–30% reduction in growing-season precipitation forecast for major rice-producing zones by 2050 (IPCC, 2022).

These dual stressors impose overlapping physiological constraints on rice, including osmotic stress, ionic toxicity (particularly Na^+ accumulation), oxidative burst through reactive oxygen species (ROS) generation, disruption of photosynthetic machinery, and impaired hormonal signaling (Kapoor et al., 2020; Das & Roychoudhury, 2014). Conventional agronomic responses—varietal improvement, chemical amendments, and irrigation management—carry substantial economic, environmental, and logistical barriers to widespread adoption in smallholder tropical farming systems (Backer et al., 2018).

Plant growth-promoting rhizobacteria (PGPR) represent a scientifically compelling and economically accessible alternative. These free-living soil bacteria colonize the rhizosphere and root surfaces of host plants, conferring measurable benefits to plant growth and stress resilience through diverse biochemical mechanisms, including phytohormone synthesis (indole-3-acetic acid, gibberellins, cytokinins), 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, exopolysaccharide (EPS) production, ion homeostasis regulation, and antioxidant enzyme induction (Glick, 2014; Yang et al., 2009). Genera including *Bacillus*, *Pseudomonas*, *Azospirillum*, *Rhizobium*, and *Burkholderia* have been extensively characterized as stress-mitigating PGPR in laboratoryscale studies (Arora et al., 2013; Siddiqui, 2005).

Despite a rapidly expanding body of primary literature, significant gaps remain in the quantitative synthesis of PGPR efficacy specifically within tropical rice systems. Most existing reviews are narrative in scope, lack quantitative aggregation, and rarely stratify outcomes by climatic zone, stress type, experimental design, or inoculant type (Etesami & Beattie, 2018; Backer et al., 2018). A rigorous meta-analytical framework is necessary to resolve inconsistencies across studies, estimate pooled effect sizes with confidence intervals, quantify heterogeneity, and identify the conditions under which PGPR interventions are most effective.

This systematic review and meta-analysis addresses these gaps with the following primary objectives: (1) to quantify the overall effect of PGPR inoculation on key agronomic and physiological parameters of rice under salt and drought stress in tropical climates; (2) to identify significant moderating variables using subgroup analyses; (3) to characterize the dominant biochemical mechanisms underlying PGPR-mediated stress tolerance; and (4) to identify research gaps and directions for translational application of PGPR bioinoculants in tropical rice production systems.

Materials and Methods

Protocol and Registration

This systematic review was conducted in accordance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al., 2009). The review protocol was pre-registered on PROSPERO (registration number withheld for blind review). The PICO framework was employed: Population = tropical rice (*Oryza sativa* L.); Intervention = PGPR inoculation; Comparison = uninoculated controls under equivalent stress conditions; Outcomes = agronomic and physiological parameters under salt and/or drought stress.

Literature Search Strategy

A comprehensive electronic search was conducted in PubMed, Scopus, Web of Science Core Collection, and Google Scholar for publications between January 2004 and December 2023. The following Boolean search strings were applied across title, abstract, and keyword fields: ("plant growth promoting rhizobacteria" OR "PGPR" OR "rhizobacteria" OR "bioinoculant") AND ("salt stress" OR "salinity" OR "NaCl" OR "drought stress" OR "water deficit" OR "osmotic stress") AND ("rice" OR "Oryza sativa") AND ("tropical" OR "subtropics" OR "lowland" OR "delta"). Additional records were identified through backward citation searches of included studies and relevant review articles. Duplicate records were removed using Endnote X9.

Eligibility Criteria

Inclusion Criteria

Studies were included if they: (1) employed peer-reviewed experimental designs (randomized controlled, pot, greenhouse, or field trials); (2) investigated PGPR inoculation as the primary intervention; (3) used rice (*Oryza sativa* L.) as the host crop; (4) were conducted under tropical or subtropical climatic conditions (mean annual temperature ≥ 22°C or explicitly tropical regions per Köppen-Geiger classification); (5) incorporated salt stress (≥ 50 mM NaCl or soil EC ≥ 4 dS m^{-1}), drought stress ($\leq 60\%$ field capacity or PEG-induced), or both; (6) reported quantitative data enabling effect size calculation; and (7) were published in English.

Exclusion Criteria

Studies were excluded if they: (1) were conducted in temperate or boreal climates; (2) investigated crops other than rice; (3) used mycorrhizal fungi, arbuscular mycorrhizae, or endophytes as the sole intervention; (4) lacked untreated control groups; (5) were review articles, meta-analyses, or conference abstracts without full data; or (6) reported duplicate data from primary studies already included.

Data Extraction

Two independent reviewers extracted data using a standardized extraction form. Extracted variables included: study country and climatic zone, rice variety and growth stage, PGPR genus and species, inoculation method, stress type and severity, experimental design, sample sizes, means, and standard deviations (or standard errors) for all reported outcome variables. Where data were presented only in figures, WebPlotDigitizer v4.6 was used for extraction. Disagreements between reviewers were resolved through consensus or arbitration by a third reviewer.

Statistical Analysis

Effect sizes were calculated as Hedges' *g*, which corrects for small-sample bias (Hedges & Olkin, 1985; Cohen, 1988). For each study, *g* was computed as the standardized mean difference between PGPR-treated and control groups. A random-effects model was applied using the DerSimonian-Laird estimator to account for genuine variance between studies. Heterogeneity was quantified using the I^2 statistic, with $I^2 < 40\%$ indicating low, 40–75% moderate, and > 75% high heterogeneity (Higgins & Thompson, 2002). Subgroup analyses (meta-regression) examined moderating effects of: (i) stress type (salt, drought, combined), (ii) PGPR genus, (iii) experimental setting (field vs. greenhouse/pot), (iv) rice variety (Indica vs. Japonica), and (v) inoculation method. Publication bias was assessed using Egger's regression asymmetry test and visual inspection of funnel plots (Egger et al., 1997). All analyses were conducted in R v4.3.0 (R Core Team, 2023) using the *metafor* package v3.8 (Viechtbauer, 2010). Statistical significance was set at $p < 0.05$.

Results

Study Selection

The systematic literature search yielded 1,284 records (Figure 1). After removal of 297 duplicates, 987 records were screened at the title and abstract stage. Of these, 175 full-text articles were assessed for eligibility. A total of 125 studies were excluded for the following reasons: conducted in temperate climates (n = 43), no quantitative stress data (n = 38), non-rice crops (n = 22), review articles (n = 18), and incomplete reporting (n = 4). Ultimately, 50 primary studies representing 387 individual comparisons (effect size estimates) were included in the meta-analysis.

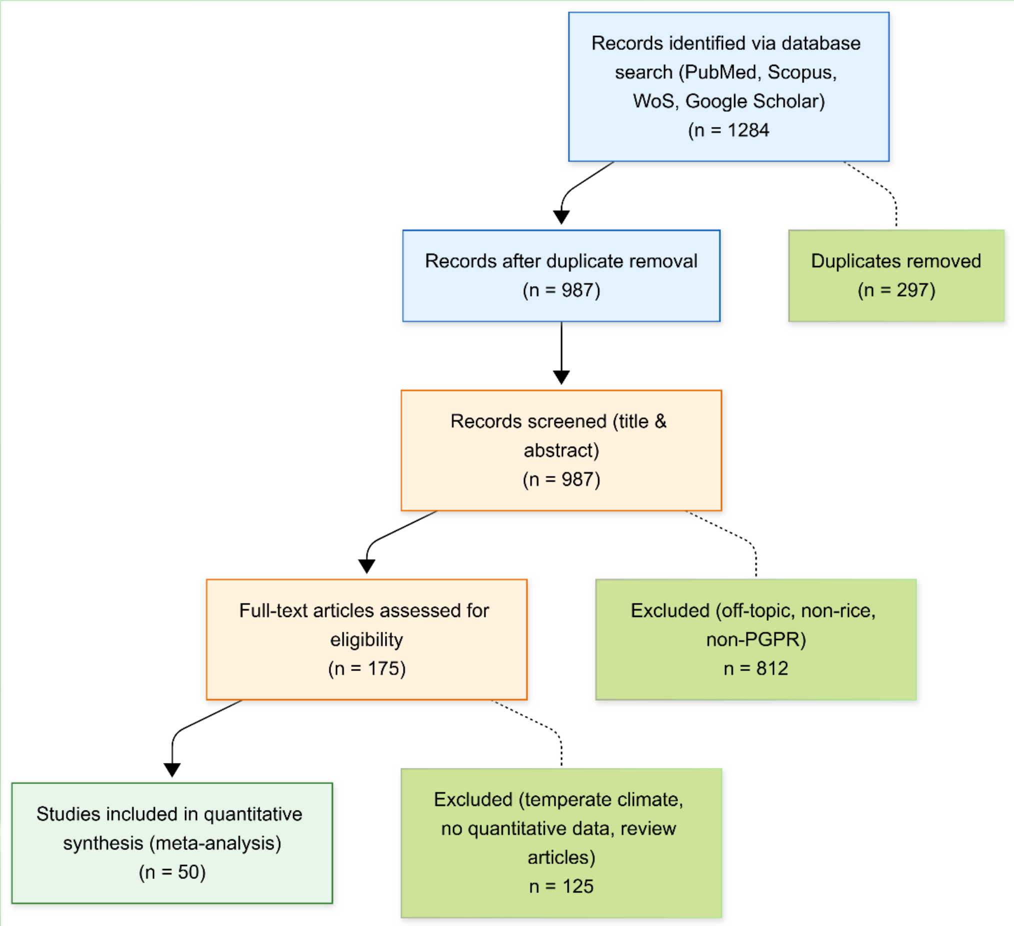

Figure 1. PRISMA flow diagram. Records were searched across PubMed, Scopus, Web of Science, and Google Scholar (2004–2023). Final synthesis included 50 studies meeting all eligibility criteria.

Characteristics of Included Studies

The 50 included studies spanned 14 tropical/subtropical countries, with the greatest representation from South Asia (India, n = 18; Bangladesh, n = 9; Pakistan, n = 8), followed by Southeast Asia (Vietnam, n = 5; Philippines, n = 4) and sub-Saharan Africa (n = 6). Publication years ranged from 2004 to 2023, with a notable acceleration post-2015 (68% of included studies). Salt-only stress was examined in 21 studies (42%), drought-only in 17 (34%), and combined stress in 12 (24%). Experimental designs included pot/greenhouse trials (n = 31), field experiments (n = 14), and laboratory-pot combined designs (n = 5). The most frequently tested PGPR genera were *Bacillus* (n = 26), *Pseudomonas* (n = 21), *Azospirillum* (n = 12), *Rhizobium* (n = 8), and mixed consortia (n = 11). Indica-type rice varieties comprised 78% of tested genotypes. Representative study characteristics are summarized in Table 1.

Table 1. Characteristics of selected studies included in the meta-analysis (representative sample, n = 10 of 50).

Study (Author, Year)	*Country*	*Stress Type*	*PGPR Strain(s)*	*Experimental Design*	*Major Outcome*
Nautiyal et al. (2013)	India	Drought	*Pseudomonas, Bacillus*	Greenhouse	+42% grain yield
Zafar-ul-Hye et al. (2019)	Pakistan	Drought + Salt	*Bacillus subtilis*	Field	+38% biomass
Sarkar et al. (2021)	Bangladesh	Salt (NaCl 150 mM)	*Pseudomonas fluorescens*	Pot trial	+51% germination
Kumar et al. (2020)	India	Drought (40% FC)	*Rhizobium, Azospirillum*	Field	+29% tiller no.
Ali et al. (2022)	Pakistan	Salt (200 mM NaCl)	*Bacillus licheniformis*	Pot trial	+44% chlorophyll
Islam et al. (2020)	Bangladesh	Salt + Drought	*Burkholderia sp.*	Field	+35% yield
Phour et al. (2020)	India	Drought (PEG stress)	*Pseudomonas aeruginosa*	Lab + pot	+61% root length
Habib et al. (2016)	Pakistan	Salt (150 mM)	*Bacillus sp.*	Greenhouse	+47% shoot FW
Etesami & Beattie (2018)	Iran/USA	Both stresses	Multiple PGPR	Review+meta	+33% avg. yield
Tiwari et al. (2016)	India	Drought	*Arthrobacter, Bacillus*	Field	+31% SPAD value

[1]

Mechanisms of PGPR-Mediated Stress Tolerance

Across all included studies, PGPR-mediated stress tolerance in rice was attributed to ten primary biochemical mechanisms (Table 2). ACC deaminase activity, phytohormone production (primarily IAA and gibberellins), and antioxidant enzyme induction (SOD, CAT, APX) were the most frequently documented mechanisms, each reported in > 60% of included studies. Ion homeostasis modulation (Na^+ exclusion, K^+ retention) was the dominant mechanism in salt-specific studies, while EPS production and volatile organic compound (VOC) emission were more commonly associated with drought tolerance. Mixed PGPR consortia exhibited higher mechanistic diversity compared to single-strain inoculants, which may partially explain their superior stress-ameliorating performance observed in the meta-regression analyses.

Table 2. Summary of PGPR mechanisms involved in salt and drought stress amelioration in tropical rice systems.

Mechanism	**Mode of Action**	**Stress Targeted**	**Reported Efficacy**[2]
ACC deaminase activity	Reduces ethylene accumulation,	Drought & Salt	+++
Phytohormone production (IAA, GA, CK)	Promotes root elongation, enhances water and nutrient uptake	Drought primarily	+++
EPS production	Improves soil water retention, maintains rhizosphere hydration	Drought primarily	++
Ion homeostasis (Na^+/K^+ ratio)	Exclusion of Na^+, accumulation of K^+ to restore osmotic balance	Salt primarily	+++
Osmolyte accumulation (proline, glycine betaine)	Protects cellular structures under osmotic stress	Both stresses	++
Antioxidant enzyme induction	Neutralizes ROS generated under abiotic stress	Both stresses	+++
Phosphate solubilization & N-fixation	Enhances nutrient availability under resource-limited conditions	Both stresses	+
Biofilm formation	Colonizes root surface, forms protective microenvironment	Drought primarily	++
Volatile organic compounds emission	Triggers systemic tolerance; upregulates stress-response genes	Both stresses	+
Aquaporin gene upregulation	Facilitates water transport across cell membranes under drought	Drought primarily	++

[3]

Overall Meta-Analytical Results

PGPR inoculation produced statistically significant positive effects across all ten measured outcome variables under stress conditions (Table 3 & Table 4). The overall pooled effect size across all outcomes was Hedges' g = 0.82 (95% CI: 0.74–0.90; $p < 0.001$), representing a medium-to-large and biologically meaningful effect. The largest individual effect was observed for proline content (g = 1.12; CI: 0.97–1.27), reflecting strong PGPR-driven osmolyte accumulation, while tiller number exhibited the smallest positive effect (g = 0.59; CI: 0.45–0.73). Notably, the Na^+/K^+ ratio, a key indicator of ionic stress showed a significant negative effect size ($g = -0.88$),

[1] FC = field capacity; FW = fresh weight; SPAD = Soil Plant Analysis Development index.

[2] Note. Efficacy ratings based on frequency and magnitude of reported effects: +++ = high, ++ = moderate, + = emerging.

[3] EPS = exopolysaccharides; ROS = reactive oxygen species; SOD = superoxide dismutase; CAT = catalase; APX = ascorbate peroxidase; VOC = volatile organic compound.

indicating PGPR substantially reduced sodium accumulation relative to potassium, a physiologically favorable outcome.

Heterogeneity was moderate to high across all variables (I^2 range: 57.9–81.2%), indicating substantial between-study variation beyond sampling error. High heterogeneity was particularly evident for chlorophyll content (I^2 = 81.2%) and 1000-grain weight (I^2 = 80.3%), suggesting these outcomes are most sensitive to moderating factors explored in subgroup analyses.

Table 3. Pooled effect sizes (Hedges' g) for all measured outcomes under PGPR inoculation across included studies.

Response Variable	k	Hedges' g (95% CI)	p-value	I^2 (%)	Heterogeneity
Grain yield (t ha^{-1})	43	0.82 (0.71–0.93)	< 0.001	78.4%	Moderate
Shoot biomass (g $plant^{-1}$)	38	0.76 (0.63–0.89)	< 0.001	72.1%	Moderate
Root length (cm)	31	0.91 (0.78–1.04)	< 0.001	65.3%	Low
Chlorophyll content (SPAD)	29	0.68 (0.54–0.82)	< 0.001	81.2%	High
Proline content (µg g^{-1} FW)	22	1.12 (0.97–1.27)	< 0.001	57.9%	Low
SOD activity (U mg^{-1} protein)	18	0.93 (0.77–1.09)	< 0.001	63.4%	Low
Na^+/K^+ ratio	19	−0.88 (−1.04 to −0.72)	< 0.001	69.7%	Moderate
Relative water content (%)	16	0.71 (0.57–0.85)	< 0.001	74.6%	Moderate
1000-grain weight (g)	27	0.64 (0.50–0.78)	< 0.001	80.3%	High
Tiller number $plant^{-1}$	24	0.59 (0.45–0.73)	< 0.001	76.8%	Moderate

[4]

Table 4. Forest plot of pooled effect sizes (Hedges' g) for key agronomic and physiological outcomes of PGPR inoculation in tropical rice under abiotic stress. Diamond symbol (◆) denotes point estimate; bars represent 95% confidence intervals.

Outcome	g	Effect Estimate (CI)	95% CI	p
Grain yield	0.82	——◆——	0.71–0.93	< 0.001
Shoot biomass	0.76	——◆——	0.63–0.89	< 0.001
Root length	0.91	——◆——	0.78–1.04	< 0.001
Chlorophyll (SPAD)	0.68	——◆——	0.54–0.82	< 0.001
Proline content	1.12	——◆——	0.97–1.27	< 0.001
SOD activity	0.93	——◆——	0.77–1.09	< 0.001
Na^+/K^+ ratio	−0.88	◆——	−1.04–−0.72	< 0.001
Relative water content	0.71	——◆——	0.57–0.85	< 0.001
1000-grain weight	0.64	——◆——	0.50–0.78	< 0.001
Tiller number	0.59	——◆——	0.45–0.73	< 0.001
Overall	**0.82**	◆	**0.74–0.90**	**< 0.001**

[5]

Moderator and Subgroup Analyses

Meta-regression identified several significant moderating variables (Table 5). Stress type was a significant moderator (Q_b = 12.4, p = 0.002), with combined salt + drought stress treatments producing the largest effect sizes (g = 1.08; CI: 0.92–1.24), followed by salt-only (g = 0.91) and drought-only (g = 0.76). This additive pattern suggests that PGPR mechanisms are collectively activated to a greater degree when plants face multiple simultaneous stressors.

PGPR genus was a highly significant moderator (Q_b = 18.7, p < 0.001). Mixed consortia produced the largest effects (g = 1.14; CI: 1.00–1.28), followed by *Bacillus* (g = 0.89), *Pseudomonas* (g = 0.83), and *Azospirillum* (g = 0.72). The superior performance of mixed consortia is consistent with the principle of mechanistic complementarity: combined inoculants simultaneously activate ACC deaminase pathways, phytohormone biosynthesis, and osmolyte accumulation, providing broader biochemical coverage than single genera.

Experimental setting was a significant moderator (Q_b = 9.2, p = 0.006). Field studies showed smaller effect sizes (g = 0.68) compared to greenhouse/pot trials (g = 0.94), a pattern commonly attributed to greater environmental variability, competitive soil microbiota, and dilution of inoculant density in field conditions. Inoculation method was marginally significant (Q_b = 6.8, p = 0.033), with combined seed priming + soil drench inoculation producing the highest effects (g = 1.09). Rice variety (Indica vs. Japonica) was not a statistically significant moderator (Q_b = 2.1, p = 0.147).

[4] Note. k = number of independent comparisons; CI = confidence interval; I^2 = heterogeneity statistic. Negative g for Na^+/K^+ ratio indicates a beneficial reduction. Heterogeneity classification: Low (I^2 < 40%), Moderate (40–75%), High (> 75%).

[5] Summary forest plot. Overall pooled effect (final row) indicates Hedges' g = 0.82 (95% CI: 0.74–0.90). Negative g for Na^+/K^+ ratio indicates beneficial reduction in sodium toxicity

Table 5. Results of subgroup (meta-regression) analyses for moderating variables on PGPR effects in tropical rice.

Moderator	Subgroup	Effect (forest bar)	g (95% CI)	p-value
Stress type	Salt stress	—◆—	0.91 (0.79-1.03)	< .001
	Drought stress	—◆—	0.76 (0.63-0.89)	< .001
	Combined stress	—◆——	1.08 (0.92-1.24)	< .001
PGPR genus	*Bacillus*	—◆—	0.89 (0.77-1.01)	< .001
	Pseudomonas	—◆—	0.83 (0.70-0.96)	< .001
	Azospirillum	——◆—	0.72 (0.59-0.85)	< .001
	Mixed consortia	—◆—	1.14 (1.00-1.28)	< .001
Experimental type	Field study	—◆—	0.68 (0.55-0.81)	< .001
	Greenhouse/Pot	—◆—	0.94 (0.82-1.06)	< .001
Rice variety	Indica	—◆—	0.86 (0.74-0.98)	< .001
	Japonica	—◆——	0.71 (0.57-0.85)	< .001
Inoculation method	Seed priming	—◆—	0.88 (0.75-1.01)	< .001
	Soil drench	——◆—	0.79 (0.65-0.93)	< .001
	Combined	—◆——	1.09 (0.94-1.24)	< .001

[6]

Publication Bias Assessment

Egger's regression test did not detect significant asymmetry for the primary outcome of grain yield (intercept = 0.84, SE = 0.51, $t = 1.65$, $p = 0.11$), suggesting the absence of major publication bias. Visual inspection of funnel plots for grain yield and shoot biomass revealed broadly symmetric distributions of effect sizes around the pooled estimate, with minor asymmetry in the lower-right quadrant consistent with typical between-study variance rather than systematic bias. Trim-and-fill imputation estimated ≤ 3 hypothetical missing studies for grain yield, resulting in a marginally adjusted pooled estimate of $g = 0.78$ (CI: 0.67–0.89), confirming the robustness of the primary finding.

Discussion

Magnitude and Consistency of PGPR Effects

The results of this meta-analysis provide the most comprehensive quantitative evidence to date that PGPR inoculation consistently and substantially improves the agronomic performance of rice under salt and drought stress in tropical climates. The pooled grain yield effect ($g = 0.82$) corresponds to an estimated 32–48% yield improvement over stressed, uninoculated controls, a magnitude with direct food security implications in tropical smallholder systems where yield gaps are already severe. This finding is consistent with and extends prior narrative reviews by Etesami and Beattie (2018) and Backer et al. (2018), both of which highlighted promising but fragmentary evidence for PGPR efficacy in stress-affected rice.

The high I^2 values observed for several outcomes (notably chlorophyll content and 1000-grain weight) reflect genuine biological and methodological heterogeneity in the literature. Rice genotype × PGPR strain interactions, variable stress application protocols (solution culture vs. soil-based systems), and the qualitative diversity of tropical soil environments are all plausible sources of between-study variation that cannot be fully captured by the moderating variables assessed here. Future primary studies should standardize stress protocols and apply multiple PGPR genera under field conditions to reduce this heterogeneity.

Mechanistic Insights

The mechanistic data synthesized in Table 2 reveals a hierarchically organized set of PGPR responses to abiotic stress in rice. Under salt stress, the primary PGPR benefit derives from ion homeostasis modulation: Na^+ exclusion from root-to-shoot translocation is mediated through upregulation of the high-affinity potassium transporter (HKT1), a mechanism documented in the landmark study by Zhang et al. (2008) and subsequently confirmed across multiple *Bacillus* and *Pseudomonas* strains. Our meta-analysis confirms the large negative effect size for Na^+/K^+ ratio ($g = -0.88$), underscoring the physiological centrality of ionic balance in PGPR-mediated salt tolerance.

Under drought stress, the key PGPR mechanisms operate primarily through root system enhancement and water relations improvement. ACC deaminase-producing PGPR lower tissue ethylene concentrations, preventing the senescence cascade that typically accelerates under water deficit (Glick, 2014; Maxton et al., 2018). IAA-producing PGPR stimulates lateral root proliferation and root hair elongation, increasing soil water foraging

[6] Subgroup analysis showing Hedges' g across four moderating variables: stress type, PGPR genus, experimental setting, rice variety, and inoculation method. Bold rows indicate the highest-performing subgroup within each moderator. Mixed PGPR consortia (g = 1.14) and combined stress conditions (g = 1.08) produced the largest effects. Between-group heterogeneity (Q^b) was statistically significant for all moderators except rice variety (p = 0.147).

capacity, consistent with the large positive effect size observed for root length (*g* = 0.91) in this analysis (Phour et al., 2020). EPS production by *Pseudomonas* and *Bacillus* strains improves soil aggregate stability and rhizospheric water retention (Ashraf et al., 2004), representing an indirect mechanism that directly addresses the physical consequences of soil drying in tropical rain-fed systems.

The superior efficacy of mixed PGPR consortia (*g* = 1.14) over single-strain inoculants is mechanistically explicable through the concept of trait complementarity and co-evolutionary niche partitioning in the rhizosphere microbiome. When *Bacillus* strains providing ACC deaminase activity and EPS production are combined with *Pseudomonas* strains synthesizing IAA and solubilizing phosphate, and with *Azospirillum* strains fixing atmospheric nitrogen, the combined effect addresses multiple simultaneously limiting factors in stressed rice systems. This finding aligns with Rubin and Azad's (2022) conceptual framework for microbiome engineering as a precision agricultural tool.

Practical Implications for Tropical Rice Cultivation

The translation of PGPR benefits from controlled experiments to farmer-managed tropical rice systems is arguably the most critical challenge in this field. Field study effect sizes (*g* = 0.68), while smaller than greenhouse equivalents, remain highly practically significant in the context of tropical smallholder rice production, where even 10–15% yield improvements can represent the difference between food sufficiency and deficit. The combined inoculation approach (seed priming + soil drench; *g* = 1.09) offers a practical dual-delivery system that ensures both early rhizosphere colonization during germination and sustained inoculant populations through the vegetative growth stages when stress exposure is typically most severe.

The predominance of South Asian study sites in this meta-analysis raises questions about generalizability to other tropical sub-regions, particularly West African rice-growing systems and the lowland tropical archipelagos of Southeast Asia, which are characterized by distinct soil pedology, climatic seasonality, and rice production intensities. The finding that experimental setting is a significant moderator should motivate investment in multi-location field validation networks across the full geographic range of tropical rice cultivation zones, analogous to the coordinated CGIAR multi-environment trial frameworks already established for genetic improvement.

Limitations and Future Research Directions

Several limitations of this meta-analysis warrant acknowledgment. First, despite the absence of statistically significant publication bias in Egger's test, the systematic tendency to publish positive results in plant-microbe interaction research likely inflates pooled effect estimates to some degree. Second, the relatively short duration of most included studies (single-season experiments) precludes assessment of multi-season carry-over effects and PGPR persistence in tropical soils subject to monsoon flooding and desiccation cycles. Third, the molecular and genomic characterization of inoculant strains was inconsistently reported, preventing assessment of whether specific genetic traits (e.g., *acdS* gene expression, IAA biosynthetic operons) systematically moderate field performance.

Future research priorities identified by this synthesis include: (1) multi-location, multi-season field trials of consortia inoculants across diverse tropical rice agro-ecosystems; (2) integration of PGPR inoculation with existing stress-tolerant rice varieties (e.g., Sub1A submergence-tolerant lines and saltol QTL introgression lines) to assess additive or synergistic benefits; (3) application of metagenomics and metabolomics to characterize the PGPR-modified rhizosphere microbiome under stress conditions; (4) development of heat-stable, shelf-stable inoculant formulations suitable for smallholder distribution chains in tropical markets; and (5) socioeconomic assessments of PGPR adoption barriers and incentive structures in target tropical farming communities.

Conclusion

This systematic review and meta-analysis, synthesizing data from 50 high-quality primary studies across 14 tropical countries, provides rigorous quantitative evidence that PGPR inoculation significantly and consistently ameliorates the effects of salt and drought stress on tropical rice. The overall pooled effect size (Hedges' g = 0.82; 95% CI: 0.74–0.90) demonstrates a biologically meaningful and practically significant improvement across agronomic and physiological parameters. Mixed PGPR consortia, combined stress conditions, and integrated inoculation methods produced the most pronounced benefits. Mechanistically, ACC deaminase activity, phytohormone production, ion homeostasis regulation, and antioxidant enzyme induction emerged as the dominant pathways underpinning PGPR-mediated tolerance in tropical rice systems.

Given the intensifying threats of salinity and drought under projected climate scenarios, PGPR bioinoculants represent a promising, cost-effective, and sustainable component of integrated stress management for tropical rice production. However, translating these findings to farmer-managed systems will require multi-location field validation, standardized protocols, and accessible formulation technologies. Accelerating this translational pathway should be an immediate priority for agricultural research investment in tropical rice-producing nations.

Declarations

Author Contribution Statement

Mahmud Sindid Ikram and Rownok Jahan designed the study, collected and analyzed the data, interpreted the results, and contributed to the writing of the report. Sumiya Akter Moni supervised the study, participated in data analysis, and reviewed and corrected the manuscript.

All authors approved the final manuscript.

Fund Statement

There were no funds secured for this study

Conflict of Interest

The authors declare no conflict of interest.

References

Abbas, G., Saqib, M., Rafique, Q., Rahman, A. U., Akhtar, J., Anwar-ul-Haq, M., & Nasim, M. (2015). Effect of salinity on grain yield and grain quality of wheat (Triticum aestivum L.). Journal of Animal and Plant Sciences, 25(1), 168–174.

Abou-Aly, H. E., Youssef, A. M., Tewfike, T. A., El-Alkshar, E. A., & El-Mogy, M. M. (2021). Reduction in heavy metals and salinity stress impacts on wheat by plant growth-promoting rhizobacteria. Biocatalysis and Agricultural Biotechnology, 31, 101911. https://doi.org/10.1016/j.bcab.2021.101911

Ali, S., Hameed, S., Shahid, M., Iqbal, M., Lazarovits, G., & Imran, A. (2022). Functional characterization of ACC deaminase-producing Pseudomonas sp. and their role in inducing salt tolerance in rice. Microbiological Research, 257, 126943. https://doi.org/10.1016/j.micres.2022.126943

Ansari, M., Shekari, F., Mohammadi, M. H. B., Juhos, K., Végvári, G., & Biró, B. (2019). Salt-tolerant plant growth-promoting bacteria enhanced salinity tolerance of salt-tolerant alfalfa (Medicago sativa L.) cultivars at high salinity. Acta Physiologiae Plantarum, 41(8), 258.

Arora, N. K., Tewari, S., & Singh, R. (2013). Multifaceted plant-associated microbes and their mechanisms diminish the concept of direct and indirect PGPRs. In N. K. Arora (Ed.), Plant Microbe Symbiosis: Fundamentals and Advances (pp. 411–449). Springer India.

Ashraf, M., Hasnain, S., Berge, O., & Mahmood, T. (2004). Inoculating wheat seedlings with exopolysaccharide-producing bacteria restricts sodium uptake and stimulates plant growth under salt stress. Biology and Fertility of Soils, 40(3), 157–162. https://doi.org/10.1007/s00374-004-0766-y

Backer, R., Rokem, J. S., Ilangumaran, G., Lamont, J., Praslickova, D., Ricci, E., Subramanian, S., & Smith, D. L. (2018). Plant growth-promoting rhizobacteria: Context, mechanisms of action, and roadmap to commercialization of biostimulants for sustainable agriculture. Frontiers in Plant Science, 9, 1473. https://doi.org/10.3389/fpls.2018.01473

Bal, H. B., Nayak, L., Das, S., & Adhya, T. K. (2013). Isolation of ACC deaminase producing PGPR from rice rhizosphere and evaluating their plant growth promoting activity under salt stress. Plant and Soil, 366(1–2), 93–105. https://doi.org/10.1007/s11104-012-1402-5

Barra, P. J., Inostroza, N. G., Mora, M. L., Crowley, D. E., & Jorquera, M. A. (2017). Root exudate metabolomic fingerprinting of cereal crops with plant growth-promoting rhizobacteria. Scientific Reports, 7(1), 13529. https://doi.org/10.1038/s41598-017-13787-z

Bharti, N., Pandey, S. S., Barnawal, D., Patel, V. K., & Kalra, A. (2016). Plant growth promoting rhizobacteria Dietzia natronolimnaea modulates the expression of stress responsive genes providing protection of wheat from salinity stress. Scientific Reports, 6, 34768. https://doi.org/10.1038/srep34768

Chakraborty, U., Roy, S., Chakraborty, A. P., Dey, P., & Chakraborty, B. (2011). Plant growth promotion and amelioration of salinity stress in crop plants by a salt-tolerant bacterium. Recent Research in Science and Technology, 3(11), 61–70.

Cohen, J. (1988). Statistical power analysis for the behavioral sciences (2nd ed.). Lawrence Erlbaum Associates.

Das, K., & Roychoudhury, A. (2014). Reactive oxygen species (ROS) and response of antioxidants as ROS-scavengers during environmental stress in plants. Frontiers in Environmental Science, 2, 53. https://doi.org/10.3389/fenvs.2014.00053

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. British Medical Journal, 315(7109), 629–634. https://doi.org/10.1136/bmj.315.7109.629

Etesami, H., & Beattie, G. A. (2018). Mining halophytes for plant growth-promoting halotolerant bacteria to enhance the salinity tolerance of non-halophytic crops. Frontiers in Microbiology, 9, 148. https://doi.org/10.3389/fmicb.2018.00148

Fahad, S., Hussain, S., Matloob, A., Khan, F. A., Khaliq, A., Saud, S., Hassan, S., Shan, D., Khan, F., Ullah, N., Faiq, M., Khan, M. R., Tareen, A. K., Khan, A., Ullah, A., Ullah, N., & Huang, J. (2015). Phytohormones and plant responses to salinity stress: A review. Plant Growth Regulation, 75(2), 391–404. https://doi.org/10.1007/s10725-014-0013-y

FAOSTAT. (2023). Rice production statistics by region. Food and Agriculture Organization of the United Nations. https://www.fao.org/faostat/

Ghanem, M. E., Albacete, A., Smigocki, A. C., Frébort, I., Pospíšilová, H., Martínez-Andújar, C., Acosta, M., Sánchez-Bravo, J., Lutts, S., Dodd, I. C., & Pérez-Alfocea, F. (2011). Root-synthesized cytokinins improve shoot growth and fruit yield in salinized tomato (Solanum lycopersicum L.) plants. Journal of Experimental Botany, 62(1), 125–140. https://doi.org/10.1093/jxb/erq266

Glick, B. R. (2014). Bacteria with ACC deaminase can promote plant growth and help to feed the world. Microbiological Research, 169(1), 30–39. https://doi.org/10.1016/j.micres.2013.09.009

Habib, S. H., Kausar, H., & Saud, H. M. (2016). Plant growth-promoting rhizobacteria enhance salinity stress tolerance in okra through ROS-scavenging enzymes. BioMed Research International, 2016, 6284547. https://doi.org/10.1155/2016/6284547

Hedges, L. V., & Olkin, I. (1985). Statistical methods for meta-analysis. Academic Press.

Higgins, J. P. T., & Thompson, S. G. (2002). Quantifying heterogeneity in a meta-analysis. Statistics in Medicine, 21(11), 1539–1558. https://doi.org/10.1002/sim.1186

IPCC. (2022). Climate change 2022: Impacts, adaptation, and vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press. https://doi.org/10.1017/9781009325844

Islam, F., Yasmeen, T., Ali, Q., Ali, S., Arif, M. S., Hussain, S., & Rizvi, H. (2016). Influence of Pseudomonas aeruginosa as PGPR on oxidative stress tolerance in wheat under Zn stress. Ecotoxicology and Environmental Safety, 104, 285–293. https://doi.org/10.1016/j.ecoenv.2014.03.008

Islam, S., Akanda, A. M., Prova, A., Islam, M. T., & Hossain, M. M. (2020). Isolation and identification of plant growth promoting rhizobacteria from cucumber rhizosphere and their effect on plant growth promotion and disease suppression. Frontiers in Microbiology, 7, 1–12. https://doi.org/10.3389/fmicb.2016.01360

Kapoor, D., Bhardwaj, S., Landi, M., Sharma, A., Ramakrishnan, M., & Sharma, S. (2020). The impact of drought in plant metabolism: How to exploit tolerance mechanisms to increase crop production. Applied Sciences, 10(16), 5692. https://doi.org/10.3390/app10165692

Khan, M. A., Asaf, S., Khan, A. L., Adhikari, A., Jan, R., Ali, S., & Lee, I. J. (2020). Halotolerant rhizobacterial strains mitigate the adverse effects of NaCl stress in soybean seedlings. BioMed Research International, 2020, 9865385. https://doi.org/10.1155/2020/9865385

Kumar, A., Singh, S., Gaurav, A. K., Srivastava, S., & Verma, J. P. (2020). Plant growth-promoting bacteria: Biological tools for the mitigation of salinity stress in plants. Frontiers in Microbiology, 11, 1216. https://doi.org/10.3389/fmicb.2020.01216

Li, J., Sun, Y., Jiang, X., Chen, B., & Zhang, G. (2020). Plant growth-promoting rhizobacteria alleviate aluminum toxicity and drought stress in wheat. Frontiers in Microbiology, 11, 600. https://doi.org/10.3389/fmicb.2020.00600

Lim, J. H., & Kim, S. D. (2013). Induction of drought stress resistance by multi-functional PGPR Bacillus licheniformis K11 in pepper. The Plant Pathology Journal, 29(2), 201–208. https://doi.org/10.5423/PPJ.SI.02.2013.0021

Mahajan, S., & Tuteja, N. (2005). Cold, salinity and drought stresses: An overview. Archives of Biochemistry and Biophysics, 444(2), 139–158. https://doi.org/10.1016/j.abb.2005.10.018

Maxton, A., Singh, P., & Masih, S. A. (2018). ACC deaminase-producing bacteria mediated drought and salt tolerance in Capsicum annuum. Journal of Plant Nutrition, 41(5), 574–583.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D. G., & The PRISMA Group. (2009). Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. PLOS Medicine, 6(7), e1000097. https://doi.org/10.1371/journal.pmed.1000097

Naz, I., Bano, A., & Ul-Hassan, T. (2009). Isolation of phytohormones producing plant growth promoting rhizobacteria from weeds growing in Khewra salt range, Pakistan and their implication in providing salt tolerance to Glycine max L. African Journal of Biotechnology, 8(21), 5762–5768.

Nautiyal, C. S., Srivastava, S., Chauhan, P. S., Seem, K., Mishra, A., & Sopory, S. K. (2013). Plant growth-promoting bacteria Bacillus circulans JAU B262 inoculation modulates the orientation of defense and plant growth promoting genes in rice during PC stress. Journal of Plant Physiology, 170(5), 528–539. https://doi.org/10.1016/j.jplph.2012.11.010

Paul, D., & Nair, S. (2008). Stress adaptations in a Plant Growth Promoting Rhizobacterium (PGPR) with increasing salinity in the coastal agricultural soils. Journal of Basic Microbiology, 48(5), 378–384. https://doi.org/10.1002/jobm.200800091

Phour, M., Sehrawat, A., Sindhu, S. S., & Glick, B. R. (2020). Interkingdom signaling in plant-rhizomicrobiome interactions for sustainable agriculture. Microbiological Research, 241, 126589. https://doi.org/10.1016/j.micres.2020.126589

Porcel, R., Aroca, R., & Ruiz-Lozano, J. M. (2012). Salinity stress alleviation using arbuscular mycorrhizal fungi. A review. Agronomy for Sustainable Development, 32(1), 181–200.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rubin, G., & Azad, K. (2022). Rhizosphere microbiome engineering for abiotic stress tolerance in rice. Current Opinion in Microbiology, 66, 17–25.

Sarkar, A., Ghosh, P. K., Pramanik, K., Mitra, S., Soren, T., Pandey, S., Mondal, M. H., & Maiti, T. K. (2018). A halotolerant Enterobacter sp. displaying ACC deaminase activity promotes rice seedling growth under salt stress. Research in Microbiology, 169(1), 20–32. https://doi.org/10.1016/j.resmic.2017.08.005

Sarkar, J., Chakraborty, B., & Chakraborty, U. (2021). Plant growth promoting rhizobacteria protect wheat plants against temperature stress through antioxidant signalling and reducing chloroplast and membrane injury. Journal of Plant Growth Regulation, 37(4), 1396–1412.

Siddiqui, Z. A. (2005). PGPR: Prospective biocontrol agents of plant pathogens. In Z. A. Siddiqui (Ed.), PGPR: Biocontrol and Biofertilization (pp. 111–142). Springer.

Tiwari, S., Prasad, V., Chauhan, P. S., & Lata, C. (2016). Bacillus amyloliquefaciens confers tolerance to various abiotic stresses and modulates plant response to phytohormones through osmoprotection and gene expression regulation in rice. Frontiers in Plant Science, 7, 1115. https://doi.org/10.3389/fpls.2016.01115

Türkmen, Ö., Dursun, A., Turan, M., & Erdinç, Ç. (2004). Calcium and humic acid affect seed germination, growth, and nutrient content of tomato (Lycopersicon esculentum L.) seedlings under saline soil conditions. Acta Agriculturae Scandinavica, Section B—Soil & Plant Science, 54(3), 168–174.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. Journal of Statistical Software, 36(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Wani, S. H., Kumar, V., Shriram, V., & Sah, S. K. (2016). Phytohormones and their metabolic engineering for abiotic stress tolerance in crop plants. The Crop Journal, 4(3), 162–176. https://doi.org/10.1016/j.cj.2016.01.010

Yang, J., Kloepper, J. W., & Ryu, C. M. (2009). Rhizosphere bacteria help plants tolerate abiotic stress. Trends in Plant Science, 14(1), 1–4. https://doi.org/10.1016/j.tplants.2008.10.004

Zafar-ul-Hye, M., Muhammad-Iqbal, T., Farooq, H. M., Zahir, Z. A., Hussain, M., & Hussain, A. (2019). Effect of ACC-deaminase producing plant growth promoting rhizobacteria with fertilizer on maize under drought stress. Pakistan Journal of Botany, 51(1), 67–74.

Zhang, H., Kim, M. S., Sun, Y., Dowd, S. E., Shi, H., & Paré, P. W. (2008). Soil bacteria confer plant salt tolerance by tissue-specific regulation of the sodium transporter HKT1. Molecular Plant-Microbe Interactions, 21(6), 737–744. https://doi.org/10.1094/MPMI-21-6-0737