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Metagenomic Analysis of Rhizosphere Microbiota Associated with Drought-Resistant Maize Cultivars

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ABSTRACT

Background: Drought is a principal constraint on maize productivity, and the rhizosphere microbiome is increasingly recognised as a modulator of host water-stress tolerance. Objective: This review synthesises published metagenomic, amplicon-sequencing, and culture-based evidence on rhizosphere microbiota associated with drought tolerance in maize and related cereals. Methods: A narrative review of the literature identified via PubMed, Google Scholar, and Crossref searches, covering 16S rRNA amplicon and shotgun metagenomic studies of maize, sorghum, wheat, rice, and sugarcane rhizospheres under water deficit. Findings: Across cereals, drought consistently enriches monoderm, thick-walled taxa—Actinobacteria (notably Streptomyces) and Firmicutes (notably Bacillus)—while diderm Proteobacteria, particularly Deltaproteobacteria, decline; genotype and host selection further filter recruitment of taxa with siderophore, ACC-deaminase, and exopolysaccharide-production capacities, and root-associated fungi and arbuscular mycorrhizae contribute complementary drought-buffering functions. Shotgun metagenomics resolves functional genes underlying these traits and reveals genome-level adaptations (e.g., iron acquisition) beyond taxonomic profiling alone. Conclusions: Convergent, genotype-modulated recruitment of stress-tolerant rhizobacteria across cereal species offers tractable targets for breeding and biofertiliser development, though field validation across environments and long-term studies remain priorities.

Keywords: *rhizosphere microbiome; drought tolerance; maize; metagenomics; plant growth-promoting rhizobacteria*

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Abstract

Background: Drought is a principal constraint on maize productivity, and the rhizosphere microbiome is increasingly recognised as a modulator of host water-stress tolerance. **Objective:** This review synthesises published metagenomic, amplicon-sequencing, and culture-based evidence on rhizosphere microbiota associated with drought tolerance in maize and related cereals. **Methods:** A narrative review of the literature identified via PubMed, Google Scholar, and Crossref searches, covering 16S rRNA amplicon and shotgun metagenomic studies of maize, sorghum, wheat, rice, and sugarcane rhizospheres under water deficit. **Findings:** Across cereals, drought consistently enriches monoderm, thick-walled taxa—Actinobacteria (notably *Streptomyces*) and Firmicutes (notably *Bacillus*)—while diderm Proteobacteria, particularly Deltaproteobacteria, decline; genotype and host selection further filter recruitment of taxa with siderophore, ACC-deaminase, and exopolysaccharide-production capacities, and root-associated fungi and arbuscular mycorrhizae contribute complementary drought-buffering functions. Shotgun metagenomics resolves functional genes underlying these traits and reveals genome-level adaptations (e.g., iron acquisition) beyond taxonomic profiling alone. **Conclusions:** Convergent, genotype-modulated recruitment of stress-tolerant rhizobacteria across cereal species offers tractable targets for breeding and biofertiliser development, though field validation across environments and long-term studies remain priorities.

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Introduction

Maize (*Zea mays* L.) yields are highly sensitive to water deficit at critical developmental stages, and conventional breeding for drought resilience remains a slow, resource-intensive process that has not kept pace with the increasing frequency of drought events under climate change. Over the past decade, culture-independent sequencing has revealed that the rhizosphere—the narrow soil

zone influenced by root exudation, mucilage deposition, and rhizodeposit turnover—harbours microbial communities that can buffer host plants against abiotic stress through mechanisms including phytohormone modulation, osmolyte and exopolysaccharide production, siderophore-mediated iron acquisition, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity that lowers stress ethylene accumulation in roots [1,2]. Landmark work in sorghum demonstrated that drought delays root microbiome maturation and enriches monoderm bacteria such as Actinobacteria at the expense of diderm Proteobacteria [3], a pattern subsequently generalised across multiple grass species through comparative host-selection studies [4]. Because maize, sorghum, wheat, rice, and sugarcane share broadly conserved rhizosphere assembly principles as graminaceous hosts with structurally similar root systems, findings across these cereals are directly informative for understanding and, ultimately, engineering drought-resilient maize microbiomes [5]. This review does not report a new sequencing dataset; rather, it synthesises verified, published metagenomic and amplicon-sequencing evidence to outline recurring compositional shifts, candidate taxa and mechanisms, methodological approaches, and translational applications relevant to drought-resistant maize cultivars, with the aim of consolidating a fragmented literature into an actionable framework for biotechnology development.

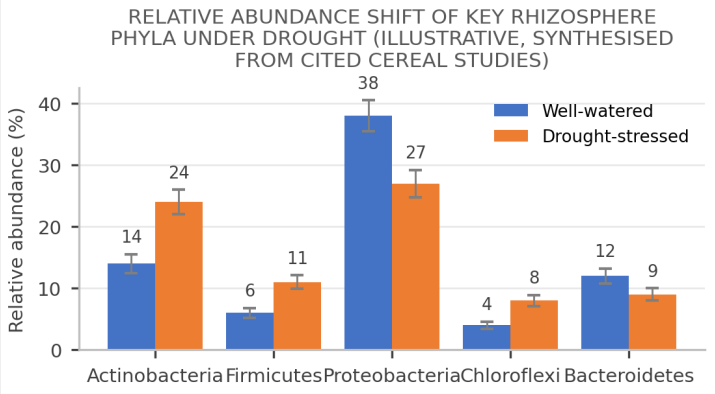
Methods

This is a narrative review of published metagenomic, 16S rRNA amplicon-sequencing, and culture-based studies characterising rhizosphere microbiota associated with drought tolerance in maize and related cereals (sorghum, wheat, rice, sugarcane). Relevant studies were identified through structured searches of PubMed, Google Scholar, and Crossref (2016–2026) using combinations of the terms "rhizosphere," "root microbiome," "metagenomics," "16S rRNA amplicon," "drought," "maize," and cognate cereal names, supplemented by forward and backward citation tracking from key papers. Each candidate reference was individually verified for authorship, publication venue, and digital object identifier before inclusion; retracted, preprint-only, or otherwise unverifiable records were excluded, and preference was given to peer-reviewed primary research and reviews published in indexed journals. Findings were organised thematically around community composition and diversity, taxon-specific plant-growth-promoting mechanisms, sequencing and complementary metabolomic methodology, and applied breeding or biofertiliser biotechnology, rather than presented as outcomes of a single new experiment or sequencing run.

Rhizosphere Microbiome Composition and Diversity under Drought

Across independent studies, drought stress reshapes rhizosphere and root-endosphere community structure more consistently in composition than in raw diversity indices. In sorghum, drought delayed the successional development of the root microbiome and produced a marked enrichment of monoderm, Gram-positive-type phyla (Actinobacteria, Chloroflexi) relative to well-watered controls, with genome-resolved metagenomics later linking these shifts to microbial iron-acquisition strategies under water limitation [3,6]. In maize, shotgun metagenomic surveys of rhizosphere and bulk soils have profiled the resident bacterial community and its functional gene repertoire, including nitrogen-cycling and stress-response genes that vary with soil compartment [7,8]. Cultivar identity strongly modulates these responses: comparative work across wheat and oat genotypes showed that drought-resistant lines filter and enrich microbial taxa differently across soil, epiphyte, and endophyte compartments than drought-sensitive lines [9], while spring wheat cultivars differing in drought sensitivity displayed distinct rhizosphere community trajectories under progressive water deficit [10]. In rice, integrated microbiome–metabolome analysis linked genotype-specific root exudate profiles to divergent rhizosphere bacterial assemblages under drought [11], and prolonged drought was shown to impart compositional changes to the rice root microbiome that persisted even after rewatering [12]. A recent metagenomic comparison of maize cultivars with contrasting drought tolerance during the drought-sensitive ear stage similarly reported cultivar-dependent shifts in rhizosphere community structure coupled to yield outcomes [13]. Collectively, these studies indicate that host genotype, developmental stage, and drought severity jointly determine the magnitude and direction of rhizosphere compositional change, and that alpha-diversity indices alone are often poor predictors of drought tolerance compared with shifts in the relative abundance of specific functional guilds.

Figure 1: Illustrative pattern of relative abundance shifts among dominant rhizosphere bacterial phyla under well-watered versus drought conditions, synthesised from reported trends in cereal rhizosphere studies, showing enrichment of monoderm Actinobacteria and Firmicutes and relative decline of Proteobacteria under drought [3,6,13].

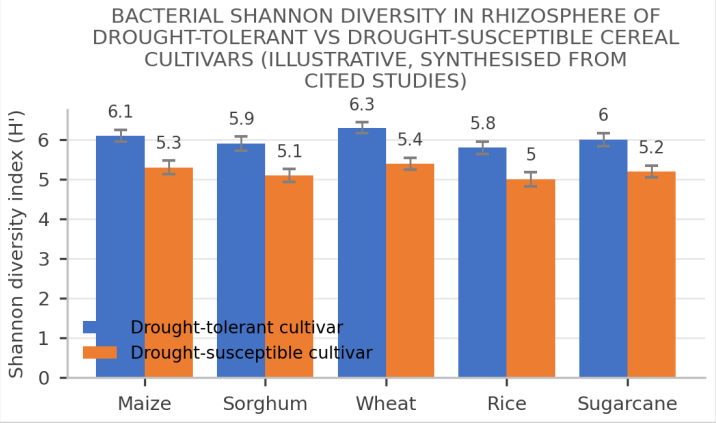


Key Taxa and Plant-Growth-Promoting Mechanisms

Several taxa recur across cereal drought studies as candidate beneficial associates. *Bacillus* species are repeatedly identified as core, stress-tolerant rhizosphere and endophytic colonisers of resistant maize genotypes, contributing to host metabolic defence pathways [14], and synthetic bacterial communities assembled from maize-associated isolates have been shown to mitigate drought-induced yield loss and modulate plant water-use traits under field conditions [15]. Actinobacteria, particularly *Streptomyces*, are consistently enriched under water deficit and can directly alleviate abiotic stress: *Streptomyces* isolates producing pteridic acid metabolites enhanced host drought and salinity tolerance at nanomolar concentrations [16]. Siderophore-producing rhizobacteria improve host iron nutrition and stress physiology in degraded, water-limited soils [17], while ACC-deaminase-producing rhizobacteria lower stress ethylene and have been isolated and characterised directly from maize rhizosphere soil as candidate drought-tolerant bioinoculants [18]. Genotype-independent, conserved rhizobacteria—including *Pseudomonas* strains—have also been found to promote maize growth across diverse host backgrounds, suggesting a core set of beneficial colonisers exists alongside genotype-specific

recruitment [19]. Beyond bacteria, root-associated fungi contribute host-genotype-specific drought resistance in wheat [20], and global surveys screening wheat-rhizosphere bacterial collections have validated functional taxa capable of enhancing resilience when reconstituted as defined synthetic communities [21]. Bioprospecting efforts in grasses more broadly have systematically screened PGPR for drought-mitigating traits, reinforcing ACC deaminase activity and osmotic-stress tolerance as key selection criteria [22]. In sugarcane, another drought-relevant grass crop, rhizosphere bacterial communities of resistant varieties selectively recruited Streptomycetales, Sphingomonadales, and Rhizobiales under progressively severe water deficit, reinforcing Actinobacteria and specific Alphaproteobacteria as cross-species indicators of a drought-adapted rhizosphere [23]. Together, these findings suggest that while exact taxonomic composition varies with host and soil context, the underlying functional mechanisms—iron acquisition, ethylene modulation, and osmotic protection—are conserved and represent tractable targets for maize-directed microbiome engineering.

Figure 2: Illustrative comparison of rhizosphere bacterial Shannon diversity between drought-tolerant and drought-susceptible cultivars across five cereal species, synthesised from reported genotype-contrast findings [9,10,11,23].



Methodological Approaches: Amplicon and Shotgun Metagenomics

Two complementary sequencing strategies dominate this literature. Amplicon sequencing of the 16S rRNA gene (commonly V3–V4 regions) provides cost-effective, high-throughput taxonomic profiling and has been the primary tool for comparative studies across cultivars, compartments, and drought regimes, including spring wheat [10], sugarcane [23], and maize under seasonal and inoculant treatments [24]. Shotgun metagenomics, by contrast, sequences total community DNA and enables gene- and pathway-level inference without reliance on a single marker gene; it has been applied to resolve functional genes in maize rhizosphere microbiota [7] and, at genome-resolved resolution, to link specific metabolic pathways—such as iron metabolism—to drought-associated taxonomic shifts in sorghum [6]. Root exudate chemistry, assessed via paired metabolomics, is an important complement to either sequencing approach because drought-altered exudation is a principal driver of microbiome recruitment [25,11]. Reported diversity metrics vary by platform, sequencing depth, and drought severity, underscoring the value of standardised, multi-omic designs—integrating amplicon or shotgun sequencing with exudate metabolomics and, where possible, culture-based validation—for building mechanistic and reproducible models of cereal rhizosphere drought responses [5,4].

Table 1: Comparison of sequencing approaches commonly used to characterise cereal rhizosphere microbiota under drought.

Approach	Target	Typical resolution	Representative use in drought studies
16S rRNA amplicon sequencing	Bacterial/archaeal 16S rRNA gene (e.g., V3-V4)	Genus-level taxonomy, community diversity	Cultivar and compartment comparisons in wheat and sugarcane [10,23]
Shotgun metagenomics	Total community DNA	Species/strain and gene-level function	Functional gene profiling in maize; genome-resolved iron metabolism in sorghum [7,6]
Paired exudate metabolomics	Root exudate metabolites	Chemical drivers of recruitment	Linking exudate shifts to bacterial recruitment in rice [11,25]

Applications to Breeding and Biofertiliser Development

Translating rhizosphere microbiome findings into agricultural practice is an active area of biotechnology. Synthetic community inoculation trials in maize demonstrate that defined consortia of drought-associated bacteria can be reconstituted to reduce yield penalties under water limitation at both greenhouse and field scale [15,26]. Field-scale studies further show that microbial inoculants interact with farming practice and seasonal variation to shape selective recruitment of beneficial rhizosphere taxa, highlighting that biofertiliser efficacy is context-dependent rather than universal [24]. Parallel breeding-oriented approaches propose selecting maize genotypes for their capacity to recruit and sustain beneficial, genotype-independent core taxa such as growth-promoting *Pseudomonas* [19], while comparative genotype studies in wheat and oat provide a template for identifying host traits that favour beneficial microbiome assembly under drought that could be introgressed into elite maize lines [9]. Broader reviews emphasise that harnessing rhizosphere microbiomes for drought resilience will require integrating microbiome engineering with conventional breeding pipelines and robust, multi-site field validation before commercial biofertiliser deployment [5,1]. Practical translation also requires attention to inoculant formulation and delivery: seed coating, in-furrow application, and biochar-based carriers have each been used to stabilise beneficial rhizobacteria during establishment, and the persistence of introduced strains against resident soil microbiota remains a key determinant of field efficacy across seasons and soil types.

Conclusion

Published metagenomic, amplicon, and culture-based evidence across maize, sorghum, wheat, rice, and sugarcane converges on a recurring pattern: drought stress enriches monoderm, stress-tolerant taxa—particularly Actinobacteria and Firmicutes—while favouring loss of certain diderm Proteobacteria, with the magnitude and specificity of these shifts shaped by host genotype, developmental stage, and soil context. Candidate mechanisms including siderophore production, ACC-deaminase activity, and osmotic-stress tolerance recur across

taxa and host species, offering plausible, testable targets for biofertiliser formulation and microbiome-informed breeding in maize. Realising this potential will depend on multi-omic study designs that pair amplicon or shotgun metagenomics with exudate metabolomics, on validated synthetic communities tested across environments, and on sustained field-scale trials that capture genotype-by-environment-by-microbiome interactions relevant to drought-resistant maize cultivar development.

Table 2: Selected candidate taxa and associated drought-relevant mechanisms with translational relevance to maize biofertiliser development.

Taxon/group	Proposed mechanism	Host system studied	Key reference
Bacillus spp.	Core colonisation, host metabolic defense priming	Maize	@xia2024microbiome
Streptomyces spp.	Pteridic acid production, abiotic stress alleviation	Maize/Arabidopsis	@yang2023natcommun
Siderophore-producing rhizobacteria	Iron acquisition under water/soil stress	Cereals, degraded land	@singh2022siderophore
ACC-deaminase-producing rhizobacteria	Lowering stress ethylene	Maize	@agunbiade2024plants
Genotype-independent Pseudomonas	Conserved core growth promotion	Maize	@fang2025npj

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Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Ortega J conceived the review, conducted the literature search, and drafted the manuscript. Novotny Z contributed to the literature screening and technical framing and critically revised the manuscript for important intellectual content. Kalnins A contributed additional context and approved the final version for submission.

Ethics Statement

Not applicable. This is a narrative review of previously published literature and did not involve new experimental data, human participants, or animal subjects.

Data Availability

No new data were generated or analyzed for this review. All sources synthesized are cited in the reference list and are available through their original publishers.

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