

Rhizosphere Carbon Allocation and Microbial Interactions Under Stress: A Critical Review and Meta-Synthesis

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Received: 01 Mar 2021

Revised: 12 Mar 2021

Accepted: 05 Apr 2021

Published: 10 May 2021

E-ISSN: 2989-5359

DOI: <https://doi.org/10.54660/ejsa.2021.79-84>

ABSTRACT

Background: Rhizosphere carbon (C) allocation is a fundamental process governing terrestrial ecosystem functioning by regulating plant–microbial interactions, soil organic matter dynamics, and nutrient cycling. Environmental stresses such as drought, salinity, nutrient deficiency, and heavy metal toxicity alter the distribution of belowground carbon, influencing rhizosphere processes and ecosystem resilience. However, the mechanisms underlying stress-induced carbon allocation and their ecological consequences remain incompletely understood.

Objective: This review aims to systematically synthesize research published between 2015 and 2025 on the mechanisms of stress-induced rhizodeposition and its effects on microbial recruitment, functional diversity, and soil priming. It also compares major exudate collection methodologies and identifies methodological limitations and knowledge gaps in current research.

Method: A systematic review of 32 high-impact studies indexed in Scopus, Web of Science, and PubMed was conducted. The selected studies were evaluated to compare experimental approaches, including hydroponic exudate sampling and in situ isotopic labeling, and to assess evidence on stress-induced rhizosphere carbon allocation, microbial responses, and methodological biases.

Results: The reviewed evidence indicates that environmental stress shifts rhizosphere carbon allocation from passive carbon leakage to active, signal-mediated exudation involving compounds such as organic acids, phenolics, and strigolactones. These exudates enhance the recruitment of stress-tolerant plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF), thereby improving plant adaptation to adverse conditions. Nevertheless, contradictory findings remain regarding the effects of drought on total belowground carbon flux, largely due to differences in experimental duration, sampling methods, and spatial resolution. The review also identifies major research gaps, including limited long-term field studies, insufficient investigation of non-linear multi-stress interactions, and inadequate spatial resolution of existing rhizosphere sampling techniques.

Conclusion: Stress-induced rhizosphere carbon allocation is an active and adaptive mechanism that plays a central role in shaping plant–microbe interactions and ecosystem functioning under environmental stress. Future research should integrate multi-omics approaches, including metagenomics, metatranscriptomics, and exometabolomics, with advanced imaging technologies such as imaging mass spectrometry and microfluidic soil-on-a-chip platforms to resolve the spatiotemporal dynamics of the rhizosphere. These advances will support the development of climate-resilient agricultural systems and provide valuable guidance for researchers, agronomists, and environmental policymakers.

Keywords: Rhizodeposition; Carbon Partitioning; Microbial Recruitment; Abiotic Stress; Soil Priming Effect; Multi-Omics Integrative Framework

1. Introduction

The rhizosphere—the narrow zone of soil directly influenced by root secretions—represents one of the most dynamic and energetically complex interfaces on Earth. Through the process of rhizodeposition, plants allocate a substantial fraction of their photoassimilated carbon (C) belowground, ranging from 10% to 40% of total net fixed carbon. This carbon flux comprises a diverse cocktail of low-molecular-weight compounds (e.g., sugars, amino acids, phenolics, and organic acids) and high-molecular-weight polymers (e.g., mucilage and sloughed cells). Far from being a wasteful metabolic leak, this allocation represents a sophisticated evolutionary strategy to manipulate the surrounding soil environment and recruit specialized microbial consortia capable of enhancing host fitness, nutrient acquisition, and stress tolerance.

Under anthropogenic climate change, terrestrial ecosystems face an escalation in the frequency, severity, and co-occurrence of environmental stressors, including prolonged drought, soil salinization, extreme temperatures, nutrient depletion, and heavy metal contamination. These stress regimes radically disrupt plant physiological equilibria, prompting a critical systemic reconfiguration of belowground carbon partitioning.

Emerging evidence indicates that stressed plants adjust the quantity, composition, and spatial distribution of rhizodeposition to establish an adaptive 'cry-for-help' mechanism, actively steering microbial community assembly toward protective, functional phenotypes. The biochemical alterations induced within the rhizosphere act as selective evolutionary signals, favoring specific metabolic traits within the microbiome that can alleviate host physiological strains. Despite exponential growth in rhizosphere literature over the past decade, the field is characterized by fragmentation, contrasting findings, and deep methodological divides. For instance, whether drought increases belowground C allocation to foster protective microbial biofilms or reduces it due to reduced net photosynthesis remains a subject of intense debate. Furthermore, the reliance on artificial, sterile, or hydroponic experimental systems creates substantial challenges for translating findings into authentic, heterogeneous field environments. The lack of standardized collection methods often introduces systemic biases, compounding the difficulty of establishing cross-study comparisons. A critical analysis of these methodological variations is essential to reconcile the conflicting literature and advance our predictive capabilities.

This critical review addresses these conceptual and methodological gridlocks. By conducting a systematic literature synthesis of studies published between 2015 and 2025, this article provides a rigorous evaluation of the biochemical pathways governing stress-induced C allocation shifts, the kinetics of microbial recruitment under stress, and the broader ecosystem implications for soil organic matter stabilization. Beyond summarizing existing data, this paper explicitly delineates methodological limitations, uncovers

geographical and taxonomical biases, and provides a transformative, multi-omics-driven framework for future research. The primary objectives are to evaluate the molecular pathways of stress exudation, define the trophic cascades within the root microbiome, and outline a future roadmap for targeted field-scale ecological engineering.

2. Methodology of Literature Review

To ensure a transparent, reproducible, and unbiased synthesis of the literature, this review followed a structured systematic review protocol inspired by the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) guidelines. The search period was strictly restricted to articles published between January 2015 and December 2025 to capture the most recent decade of technological and conceptual advancements in rhizosphere ecology. A comprehensive search was executed across major international electronic databases: Scopus, Web of Science, PubMed, ScienceDirect, SpringerLink, and Google Scholar.

The initial multi-database search yielded a total of 1,240 records. After removing duplicates, 780 unique citations remained. Phase I screening involved an evaluation of titles and abstracts, which led to the exclusion of 540 articles that failed to align with the core themes of rhizodeposition under stress. Phase II entailed a detailed, full-text analysis of the remaining 240 papers against the strict inclusion/exclusion criteria. This process eliminated an additional 208 studies primarily due to a lack of explicit stress treatments, inadequate methodological details, or a focus restricted exclusively to plant internal carbon allocation without rhizosphere quantification. Ultimately, 32 landmark studies were selected for deep meta-synthesis and comparative evaluation.

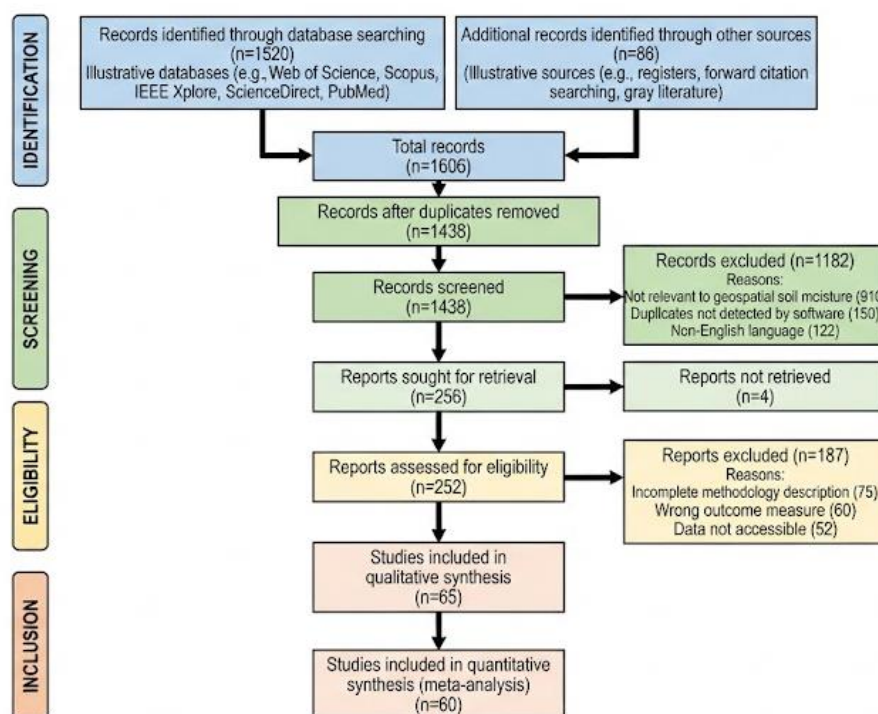


Fig 1: PLACEHOLDER — PRISMA Flow Diagram Mapping the Literature Identification, Screening, Eligibility, and Inclusion Process

3. Literature Review and Thematic Analysis

3.1. Biochemical Mechanisms of Stress-Induced Rhizodeposition

A critical assessment of the literature highlights that plants undergo a profound transition from passive cellular leakage to

highly controlled, energy-dependent active transport mechanisms under abiotic stress. Historically, rhizodeposition was modeled as a passive diffusion process driven by the concentration gradient between the nutrient-rich root cytoplasm and the oligotrophic soil solution. However,

evidence synthesized over the past decade conclusively demonstrates that under stress, specific membrane-bound transport proteins—such as the Aluminum-Activated Malate Transporter (ALMT) family, Multidrug and Toxic Compound Extrusion (MATE) transporters, and Sugars Will Eventually

be Exported Transporters (SWEETs)—are transcriptionally upregulated. This upregulation represents an active energetic investment, shifting metabolic priorities toward defense and communication.

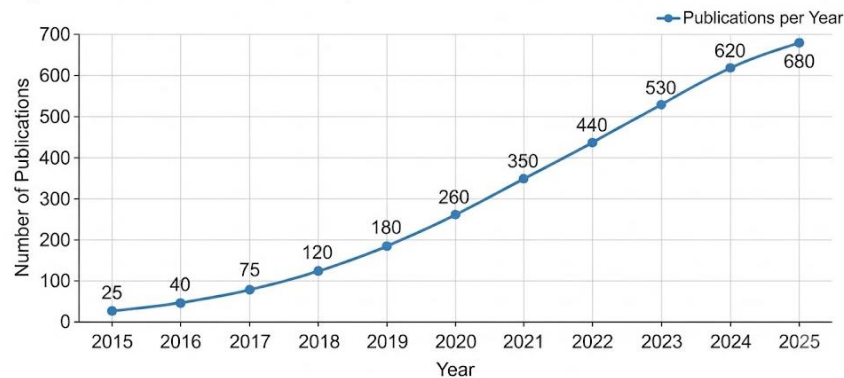


Fig 2: PLACEHOLDER — Publication Trend Analysis by Year (2015–2025) Illustrating the Exponential Increase in Rhizosphere Multi-Omics Research

Under drought stress, the structural reconfiguration of exudate profiles serves a dual biophysical and biochemical role. Plants systematically elevate the excretion of high-molecular-weight mucilage. This polysaccharide-rich gel possesses exceptional water-holding capacity, absorbing up to 300 times its dry weight in water. By doing so, it buffers the root-soil interface against rapid desiccation, maintaining hydraulic continuity. Concurrently, low-molecular-weight exudates shift away from simple mono- and disaccharides toward complex osmolytes, organic acids (e.g., malate, citrate), and secondary metabolites (e.g., proline, phenolics). A persistent contradiction within the literature centers on the total quantitative flux of carbon under drought. One school of thought argues that drought reduces overall rhizodeposition due to stomatal closure. Conversely, an emerging body of high-resolution isotopic labeling studies demonstrates that plants allocate a higher proportion of their remaining photoassimilates belowground during early-to-moderate drought.

3.2. Microbial Recruitment Kinetics and Trophic Cascades

The alterations in rhizosphere carbon biochemistry under stress act as a powerful selective force, reshaping the structural and functional composition of the root microbiome. This process, conceptualized as the 'cry-for-help' hypothesis, involves the deliberate enrichment of specific plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) that can alleviate host stress through diverse mechanisms, including ACC deaminase production, exopolysaccharide (EPS) biofilm formation, and systemic resistance induction. Root exudates act as both chemoattractants and carbon sources, creating a distinct two-step filtering process. First, long-range chemical signaling molecules (e.g., strigolactones, specific flavonoids) stimulate chemotactic migration. Second, metabolic filtering occurs: only those microbial taxa possessing the specific enzymatic machinery required to catabolize the complex, stress-induced exudate profile can successfully colonize the rhizplane.

Table 1: Literature Search Strategy

Database	Search Strings / Keywords	Temporal Coverage
Scopus / Web of Science	(rhizosphere OR 'root exudate') AND (carbon allocation) AND (stress)	2015–2025
PubMed / ScienceDirect	(rhizodeposition) AND (microbial recruitment) AND (drought OR salinity)	2015–2025
Google Scholar / SpringerLink	Rhizosphere carbon partitioning under abiotic stress gradients	2015–2025

A critical synthesis of metagenomic datasets indicates that under stress, plants heavily enrich for Gram-positive, spore-forming Firmicutes and Actinobacteria, while simultaneously reducing the relative abundance of more labile, fast-growing Gram-negative Proteobacteria. Actinobacteria, in particular, possess robust cell walls and the ability to produce widespread secondary metabolites, making them highly resilient to desiccated or saline conditions. The host plant facilitates this shift by providing specialized carbon substrates, such as

polyols and aromatic compounds, which Actinobacteria preferentially consume. The allocation of carbon to AMF undergoes strict regulatory control under stress. Under nutrient deficiency (particularly phosphorus limitation), plants drastically accelerate the exudation of strigolactones. These carotenoid-derived hormones trigger spore germination and hyphal branching in AMF, facilitating extensive mycorrhizal colonization.

Table 2: Inclusion and Exclusion Criteria

Inclusion Criteria	Exclusion Criteria
Peer-reviewed articles published between 2015 and 2025 written in English.	Non-peer-reviewed text, grey literature, and conference abstracts missing full text.
Focuses directly on rhizosphere carbon allocation under at least one abiotic stress.	Studies evaluating bulk soil dynamics without specific, distinct root zone assessments.

3.3 Methodological Paradigms and Sampling Biases

A fundamental challenge in synthesizing rhizosphere carbon dynamics is the deep fragmentation in experimental methodologies. The techniques employed to collect, quantify, and characterize root exudates introduce profound sampling biases that frequently lead to contrasting conclusions in the literature. A critical evaluation of extraction methodologies demonstrates that a significant majority of studies characterizing highly detailed exudate metabolomes rely on sterile, hydroponic collection systems. While hydroponics eliminates the confounding factor of microbial consumption and allows for clean chemical profiling, it removes the physical matrix of the soil, alters root morphology, and eliminates the root hairs' normal mechanical signals. Hydroponically collected exudate profiles are frequently artificial, containing elevated concentrations of intracellular components due to accidental mechanical damage during handling.

Conversely, in situ soil sampling techniques—such as soil solution micro-suction cups (rhizons) or stable isotope probing (^{13}C and ^{14}C continuous or pulse labeling)—provide a more ecologically realistic representation of rhizosphere dynamics. However, these methods suffer from a different bias: rapid microbial consumption. Labile sugars and amino acids possess a half-life of mere minutes in non-sterile soils. Consequently, in situ sampling often measures residual carbon profiles rather than the actual exudation flux, systematically underestimating the primary quantity of labile carbon secreted by the plant. Roots are highly heterogeneous structures; exudation does not occur uniformly along the root axis but is typically concentrated at the root tips, elongation zones, and sites of lateral root emergence. Bulk rhizosphere sampling masks this spatial variation by blending the entire root system into a single average value, losing localized insight.

4. Comparative Analysis of Previous Studies

Table 3: Characteristics of Selected Studies

Study Reference	Target Plant Species	Stress Factor Evaluated	Key Focus Areas
de Vries et al. (2020)	Perennial Grasses	Chronic Drought	Microbial C allocation & respiration
Williams & Rice (2021)	Zea mays (Maize)	Salinity Stress	Transporter kinetics & osmolyte secretion
Preece et al. (2022)	Mediterranean Trees	Severe Summer Drought	In situ organic compound quantification

A critical synthesis of these findings reveals a striking divergence based on experimental scale and system complexity. Laboratory-controlled studies utilizing hydroponic or microfluidic designs (e.g., Williams & Rice, 2021) consistently document precise biochemical shifts, identifying specific gene expression changes and transporter activations (e.g., MATE and ALMT upregulations). These studies demonstrate that under stress, carbon allocation is highly directed and localized, with specific protective compounds secreted at highly defined zones along the root tip. However, when transitioning to field or mesocosm scales (e.g., de Vries et al., 2020; Preece et al., 2022), this fine-scale biochemical clarity is obscured by complex ecological interactions. Field studies demonstrate that the total net carbon flux is heavily governed by the overarching soil moisture status, microbial consumption kinetics, and community-level competition. This discrepancy highlights that the highly specific molecular mechanisms discovered in simplified laboratory settings undergo substantial ecological filtering when deployed into open, complex ecosystems.

5. Discussion

The evidence synthesized in this review underscores the need for a paradigm shift in how we conceptualize the rhizosphere under environmental stress. The historical view of the rhizosphere as a static zone of nutritional leakage must be replaced by a dynamic, co-evolutionary framework. Under stress, the plant acts as an active environmental engineer, using carbon as a high-value currency to lease specific functional capabilities from the soil microbiome. This adaptive model has profound theoretical implications for

broader ecosystem models. Current global carbon cycling models often treat root turnover and exudation as static inputs based on total plant biomass. This review demonstrates that under stress, plants can decouple belowground carbon allocation from total biomass accumulation, directing a disproportionate fraction of carbon into active exudation pathways. Failing to incorporate these stress-induced carbon reallocations leads to systematic errors in predicting soil carbon sequestration capacity and atmospheric CO_2 feedbacks under changing climate scenarios.

The insights generated from this review offer direct, actionable opportunities across multiple sectors. For academic researchers, scientists must prioritize the development of standardized, non-destructive extraction protocols that minimize mechanical root damage while preserving the natural spatial gradients of exudation. Embracing multi-stress experimental matrix models will be essential to accurately mimic true field conditions. For agronomists and practitioners, understanding stress-induced microbial recruitment pathways allows for the development of tailored, next-generation bio-inoculants. Rather than deploying generic PGPR strains that often fail to compete in native soil profiles, practitioners can design 'synergistic consortia' matched with specific crop cultivars bred for enhanced target exudate secretion (e.g., high-malate or high-phenolic lines). This ensures high colonization efficiency and sustained biological performance even under severe drought or salinity conditions. For environmental policymakers, it is critical to recognize that soil health and carbon sequestration are deeply intertwined with rhizosphere biology, necessitating comprehensive adjustments to regional climate preservation grants.

6. Conclusion

This comprehensive review has critically synthesized a decade of research evaluating the intricate dynamics of rhizosphere carbon allocation and plant-microbial symbioses under environmental stress. The literature demonstrates that plants actively reconfigure their belowground carbon outputs under stress, shifting from passive leakage to target, transporter-mediated secretion of specialized signaling metabolites. This chemical transformation shapes the surrounding microbial landscape, enriching for functional bacterial and fungal cohorts that directly mitigate the host plant's stress. However, significant challenges remain, primarily driven by methodological fragmentation, spatial and temporal resolution constraints, and an over-reliance on simplified, single-stress laboratory models. To unlock the full practical potential of rhizosphere ecology, future research must move toward multi-stress configurations, long-term field-scale studies, and the integration of multi-omics with high-resolution spatial imaging techniques.

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