

Original article

Soil and Root-Associated Microbial Responses to Abiotic Stress under Climate Change: Implications for Carbon Cycling, Plant Resilience, and Microbial Bioinoculants

Abu Bakr Alzahaf^{1*} , Gazala Saad² 

¹Department of Botany, Faculty of Science, University of Tobruk, Tobruk, Libya

²Department of Plant Protection, Faculty of Agriculture, Omar Al-Mukhtar University, Al Bayda, Libya

Email: abubakr.sulaiman@tu.edu.ly

Abstract

Soil and root-associated microbial communities are pivotal to terrestrial biogeochemical cycling; however, compounding global change stressors increasingly compromise their structural and functional resilience. This review synthesizes microbial responses to key abiotic perturbations, including elevated atmospheric CO₂ (eCO₂), thermal anomalies, hydrological extremes (drought and flooding), and nutrient imbalances (N and P). We critically evaluate how these factors regulate microbial carbon use efficiency (CUE), greenhouse gas emissions, and the distribution of metabolic traits, specifically the balance between fast-growing (r-strategists) and slow-growing (K-strategists) populations. We also explore mechanisms of plant-microbe interactions under stress, focusing on root exudation patterns and phytohormone signaling (e.g., ethylene modulation via ACC deaminase). By bridging microbial physiology, metagenomics, and trait-based ecology, this study underscores the critical need to parameterize soil microbial mechanisms into climate feedback models to advance ecosystem management, ensure crop resilience, and improve the efficacy of soil bioinoculants.

Keywords. Global Change, Soil Microbiome, Microbial Carbon Use Efficiency, Plant-Microbe Interactions.

Introduction

Soil constitutes one of the most biodiverse ecosystems on Earth, harboring complex interacting networks of bacteria, archaea, viruses, fungi, and protozoa—collectively termed the soil microbiome. This biome exists within a highly heterogeneous abiotic matrix characterized by disconnected air- and water-filled pores, alongside patchy nutrient distributions that form distinct microbial hotspots [1]. The confluence of biotic influences (e.g., plant roots and soil fauna) and fluctuating abiotic variables (e.g., moisture, temperature, and redox potential) renders the soil environment inherently dynamic. However, anthropogenic climate change is driving unprecedented extremes in these environmental parameters, raising critical uncertainties regarding the stability and resilience of the soil microbiome [2]. Elucidating microbial life-history strategies—such as the relative abundance of fast-growing, opportunistic r-strategists versus slow-growing, competitive K-strategists—alongside localized edaphic properties are therefore essential for predicting microbiome trajectories under future climate scenarios [3].

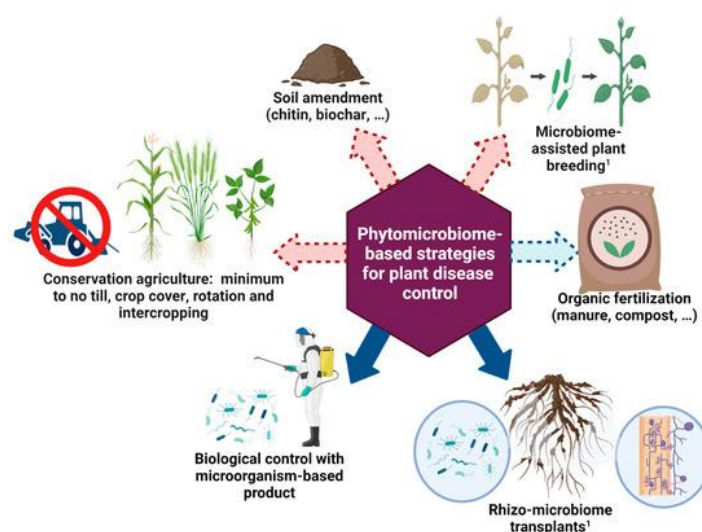


Figure 1. Soil and Phyto microbiome for Plant Disease Suppression and Management under Climate Change

Climate change and soil-climate feedback

Over the past century, sustained increases in atmospheric CO₂ and global temperatures have altered baseline climatic conditions. As projected by recent national and international climate assessments, these shifts are accelerating towards more erratic and extreme weather events [4]. Because soil microorganisms are the primary regulators of soil organic carbon (SOC) and nutrient cycling, they dictate the magnitude and direction of climate feedbacks, fundamentally controlling the production and consumption of greenhouse gases (GHGs) such as CO₂, CH₄, and N₂O. Despite this, predicting whether soils will act as net GHG sources or sinks under future climates remains highly challenging [5,6]. This uncertainty stems from complex, spatially variable shifts in soil carbon and nitrogen pools, as well as divergent microbial responses across different environments. Consequently, while the pivotal role of microbial ecology in climate projections is widely acknowledged, successfully parameterizing these processes into landscape-scale Earth system models remains an unresolved challenge [7].

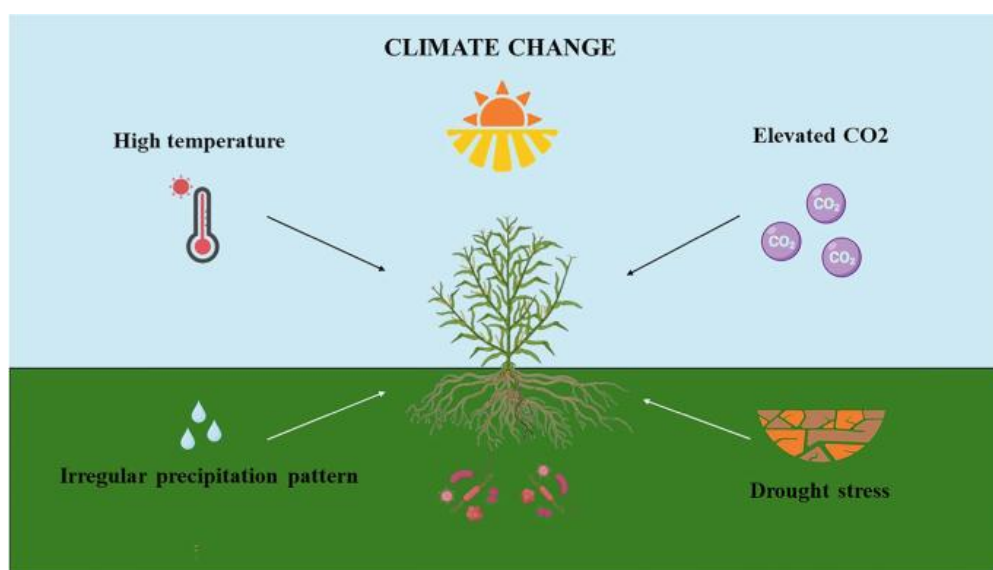


Figure 2. Effect of Climate Change on Beneficial Plant–Microbe Interaction in the Rhizosphere

This review synthesizes current literature on soil microbial responses to primary climate change drivers: elevated atmospheric CO₂ (eCO₂), warming, drought, altered precipitation regimes (including flooding), and compounding extreme events [8]—such as concurrent heatwaves and eCO₂ [9], or synergistic drought-warming effects [10]. Understanding these complex interactions is crucial for evaluating how climate-driven pressures impact the ecosystem services provided by microbial communities, thereby informing strategies to protect, manage, and enhance ecosystem resilience. A critical concern is that climate change may accelerate microbial SOC mineralization, thereby creating a positive feedback loop that exacerbates warming. The global soil carbon reservoir, encompassing permafrost, is estimated at ~3,300 Pg—roughly five times the current atmospheric CO₂ pool [11,12]. Yet, the trajectory of this vast carbon pool under future climates remains highly debated. Traditionally, field-based climate change studies have relied heavily on soil respiration metrics; however, accurately modeling soil carbon-climate feedbacks requires robust empirical data on how bulk soil carbon stocks respond to climatic shifts [13].

Soil microorganisms govern a dichotomy: they mineralize SOC while simultaneously stabilizing exogenous carbon inputs. The balance of these processes determines the net atmospheric flux of CO₂ and CH₄. The proportion of assimilated carbon allocated to microbial biomass versus lost as CO₂ is defined as microbial carbon use efficiency (CUE). Although climate change has globally stimulated heterotrophic SOC respiration [14], subsequent carbon losses could potentially be offset by enhanced plant-derived carbon inputs [15] and microbial autotrophic fixation. Furthermore, the temperature sensitivity of SOC decomposition is highly contingent on litter chemistry and existing SOC molecular structure [16]. Thus, local biogeochemical contexts profoundly shape microbial metabolic responses to climate drivers. A pressing priority for Earth system models is the mathematical integration of microbial ecological traits that dictate ecosystem-level CUE and its feedback with climate forcing. Nitrogen (N) cycling is inextricably linked to climate regulation due to its tight coupling with CO₂, N₂O, and CH₄ dynamics [17].

Mitigating soil N₂O emissions is particularly urgent; N₂O possesses a global warming potential 298 times that of CO₂, with soils contributing 56–70% of global emissions [18]. Managing these emissions is complicated by the metabolic diversity of N-cycling communities [19] and the high spatiotemporal variability of soil redox conditions [20,21]. The discovery of

complete ammonia oxidizers (comammox), which oxidize ammonia to nitrate without N₂O by-products and are highly abundant in soils [22,23], highlights how resolving microbial physiology and metabolic pathways is fundamental to predicting N-cycle responses to a changing climate.

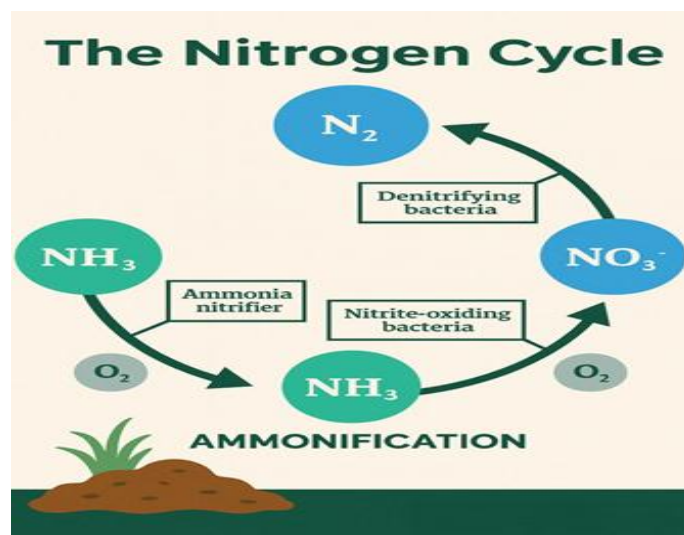


Figure 3. Nitrogen (N) cycle

Microbial responses to discrete abiotic stressors

Elevated CO₂. Long-term Free-Air CO₂ Enrichment (FACE) experiments across diverse biomes have provided critical insights into microbial responses to eCO₂. These studies reveal both ecosystem-specific and conserved phylogenetic shifts; for instance, a decade-long cross-biome study identified a universal increase in Acidobacteria under eCO₂ [24], while Australian grasslands demonstrated shifts in archaeal, fungal, and specific bacterial assemblages [25]. Translating these phylogenetic shifts into ecological traits requires a trait-based framework [26]. Metagenomic analyses have elucidated functional shifts under eCO₂: the BioCON experiment reported elevated gene families associated with decomposition, nitrogen fixation, and dissimilatory nitrate reduction, alongside decreased abundance of genes involved in glutamine synthesis and anammox [27]. Similarly, in arid grasslands, eCO₂ upregulated microbial genes for decomposition, carbon fixation, CH₄ metabolism, and denitrification [28]. Increased temperature. The resilience of microbial communities to warming is modulated by interacting factors, particularly drought and vegetation type. The 12-year Prairie Heating and CO₂ Enrichment (PHACE) experiment in Wyoming grasslands demonstrated that while eCO₂ alone or combined with warming enriched carbon and nitrogen cycling genes, warming alone suppressed N-cycling pathways [29]. Crucially, positive plant community responses (increased biomass) compounded precipitation shifts [30].

Consequently, while warming accelerated both soil carbon inputs and respiration, carbon losses via respiration were largely offset by enhanced plant biomass, weakening the positive feedback to climate warming and mitigating soil carbon loss. This challenges the prevailing paradigm in most climate models, which predict a strong positive feedback driven by warming-induced respiration and depleted soil carbon stocks [31]. Drought. Soil microorganisms employ diverse physiological strategies to navigate water stress, including osmoregulation, dormancy, and the synthesis of extracellular enzymes [32]. To maintain cellular turgor under declining water potentials, microbes accumulate osmolytes, though this strategy can become energetically prohibitive under severe drying [33,34]. Alternatively, microorganisms may enter a desiccated dormant state, reactivating upon moisture availability [35]. The production of extracellular polymeric substances (EPS) is another critical adaptation for retaining water under low matric potentials. Taxonomically, groups such as Actinobacteria and Bacilli exhibit heightened persistence in drought-impacted soils due to their capacity to sustain low metabolic activity and enter dormant states [36,37]. Altered precipitation, flooding, and compounding fire disturbances. Wetlands serve as critical terrestrial-aquatic interfaces and are highly sensitive to climate regimes. CH₄ dynamics in these systems are governed by soil temperature, water-table depth, and SOC composition [38]. Under future climates, peatlands risk transitioning from carbon sinks to sources, though episodic flooding can inhibit oxidative SOC decomposition, resulting in temporary net carbon uptake.

A compounding factor is sea-level rise, which drives saltwater intrusion into coastal soils at an estimated rate of 3.2 ± 0.4 mm per year [39]. The introduction of sulfate via saltwater acts as a terminal electron acceptor, altering redox dynamics and subsequently increasing soil microbial biomass [40]. Furthermore, fire acts as a severe compounding disturbance. Its impact on SOC and the microbiome is dictated by topography and plant inputs. In boreal regions, intense fires can thaw

underlying permafrost, leading to hydrological drainage of slope soil carbon [41]. Paradoxically, fire-derived charcoal is highly stable and has been shown to sustain nitrifying bacterial activity post-fire [42]. Fire also induces soil alkalization—a primary driver of microbial diversity—causing an initial post-fire increase in fungal diversity that declines over time [43]. When fire coincides with extremes like drought, microbiome resilience is severely compromised [44], though generalized predictions are hindered by the inherent fire-resilience of certain ecosystems, such as biological soil crusts in adapted grasslands [45].

Flooding stress: Plant-microbe interactions in the rhizosphere

While water is fundamental to life, prolonged inundation severely stresses most terrestrial crops, a frequency expected to increase with climate change [46,47]. Submergence of non-photosynthetic roots rapidly depletes O₂, inhibiting cellular respiration and triggering severe physiological stress. A hallmark of this response is the rapid accumulation of ethylene, a stress-signaling phytohormone that detrimentally alters shoot and leaf morphology [46,48]. Characterizing rhizosphere microbial dynamics under flooding is critical for identifying plant growth-promoting (PGP) microbes capable of conferring hypoxia tolerance. A primary mechanism involves bacterial production of 1-aminocyclopropane-1-carboxylate (ACC) deaminase. By cleaving ACC—the immediate biochemical precursor to ethylene—these bacteria lower plant ethylene levels, thereby mitigating stress-induced damage [49,50]. For instance, basil (*Ocimum sanctum*) inoculated with ACC deaminase-producing bacteria exhibited enhanced growth and reduced ethylene accumulation under waterlogged conditions compared to controls [51]. Similarly, proteomic profiling of cucumber (*Cucumis sativus*) inoculated with *Pseudomonas putida* UW4 under hypoxia revealed an upregulation of proteins involved in nutrient metabolism, defense, and antioxidant activity, elucidating the mechanisms behind bacterial stress amelioration [52].

Despite this clear potential, few studies have characterized root-associated microbial community shifts in non-wetland, especially crop, species under flooding. Existing research focuses exclusively on bacterial communities. For example, T-RFLP profiling of poplar (*Populus* sp.) seedlings subjected to experimental flooding revealed profound compositional shifts in the rhizosphere and root compartments, largely driven by a marked increase in taxa affiliated with the genus *Aquaspirillum* [53]. In wheat (*Triticum aestivum*), the compounding stress of flooding and nitrogen limitation altered denitrifier community structures in the rhizosphere relative to bulk soil [59]. Under hypoxic conditions, plant roots also exude phytotoxic compounds—such as ethanol, lactic acid, and alanine—as byproducts of fermentative metabolism, a mechanism to prevent cellular damage [54–58]. However, the influence of these phytotoxic exudates on root-associated bacterial assemblages remains largely unexplored. Addressing this gap, Graff and Conrad [59] hypothesized that the previously observed proliferation of *Aquaspirillum*—a genus encompassing known ethanol-catabolizing species [60]—may be directly stimulated by the ethanol exuded by hypoxic plant roots, highlighting a complex, stress-dependent metabolic feedback loop within the rhizosphere.

Drought

Operationally defining drought remains complex due to its reliance on historical precipitation baselines [61]; however, in the context of plant-microbe interactions, it is characterized by soil water deficits that induce physiological stress in host plants. Compared to flooding, drought has been extensively studied as a primary driver of soil and root-associated microbiome assembly (for comprehensive analyses, see Naylor and Coleman-Derr [62]). Drought imposes systemic perturbations across both edaphic and plant domains. Generally, bacterial responses in the rhizosphere mirror those in bulk soil, predominantly characterized by an enrichment of Gram-positive (Gr+) and monoderm taxa, particularly Actinobacteria. Crucially, an expanding body of evidence indicates that drought-induced metabolic and morphological alterations in plant roots significantly modulate microbiome composition.

This dichotomy underscores the necessity of including unplanted soil controls to decouple the direct physicochemical impacts of desiccation on microbes from the indirect, plant-mediated effects. Future research utilizing mutant or naturally drought-tolerant plant accessions will be instrumental in elucidating the specific microbial taxa that confer host resilience, thereby facilitating the discovery of novel bioinoculants. For instance, root-associated microbiomes have been shown to enhance drought tolerance in sorghum [63], potato [64], and maize [65]. Additional examples include root bacteria isolated from arid environments improving photosynthesis, stomatal conductance, and biomass in pepper (*Capsicum annuum*) [66], and the PGP fungus *Piriformospora indica* augmenting chlorophyll content and priming drought-responsive genes in *Arabidopsis thaliana* [67,118]. While such microbes represent promising inoculants, their field efficacy is contingent upon their rhizosphere competence and ability to navigate complex competitive interactions with indigenous microbiomes [68]. Consequently, continued genomic characterization of crops is imperative to unravel the genetic regulators governing root microbiome assembly under water-limited conditions, ultimately enabling the breeding of crop genotypes optimized for maximal responsiveness to targeted microbial inoculants [69].

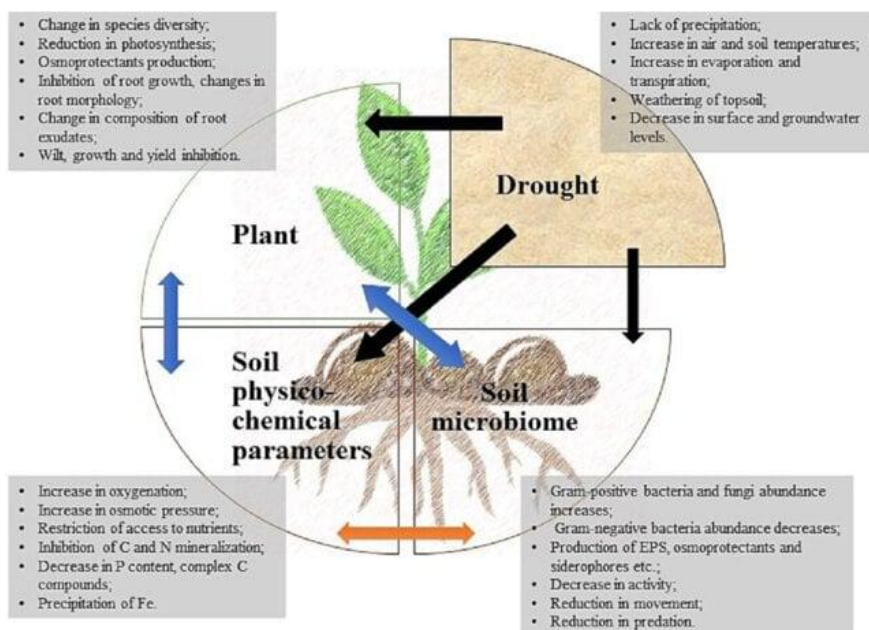


Figure4. Effect of drought on soil, microbiome, and plant relationships

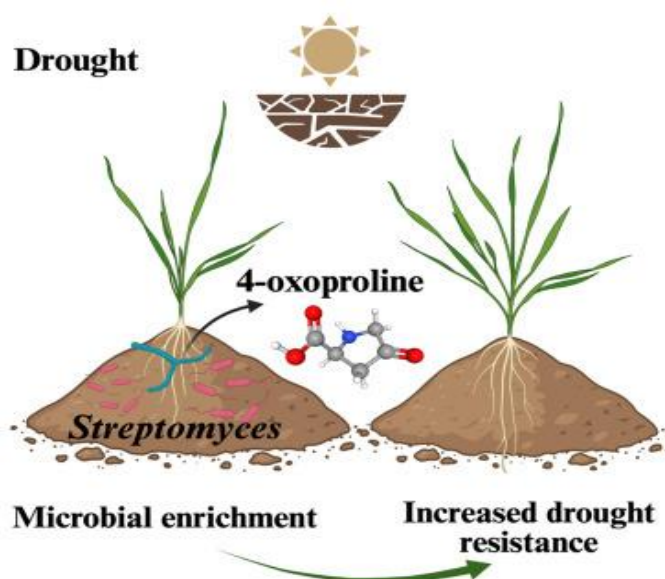


Figure 5. Drought-induced plant microbiome and metabolic enrichments improve drought resistance

Nitrogen

Nitrogen (N) is a fundamental element for all life and a primary limiting nutrient in terrestrial ecosystems [70,71]. Because the bulk of environmental N exists as inert dinitrogen (N₂), the advent of the Haber–Bosch process revolutionized agriculture by supplementing biological nitrogen fixation (BNF) with synthetic fertilizers, precipitating massive increases in global biomass and grain yields [72]. Beyond agronomic yields, however, the application of synthetic N profoundly alters the phyto-microbial interface, primarily through the modulation of root exudation profiles. For example, Kavamura et al. [73] demonstrated that rhizosphere bacterial communities of unfertilized wheat were functionally enriched for terpenoid metabolism pathways and depleted in carbohydrate and amino acid metabolism genes. Given that terpenoids act as biological nitrification inhibitors [74,75], their exudation under low N conditions may represent an active plant strategy to mitigate N loss, though it remains unclear whether nitrification inhibition is a targeted adaptation or a secondary metabolic consequence [155].

Conversely, Zhu et al. [76] showed that in maize, progressive increases in N availability positively correlated with the root exudation of sugars, sugar alcohols, and phenolics. This exudative shift drove increases in bacterial abundance (16S rRNA gene copy number) and the relative enrichment of nitrifying and denitrifying genes. The resulting metabolic shift in the

rhizosphere was associated with reduced nitrogen use efficiency (NUE) and elevated fertilizer N losses under high N inputs. At the transcriptional level, Carvalhais et al. [77] illustrated how low-N root exudates actively modulate microbial behavior. When the PGP bacterium *Bacillus amyloliquefaciens* FZB42 was exposed to exudates from N-deficient maize, transcriptomic analyses revealed a downregulation of protein synthesis genes—indicative of a general stress response, potentially induced by a lack of amino acids or the presence of allelochemicals. Furthermore, because this specific *Bacillus* strain facilitates phosphorus rather than nitrogen acquisition, the observed downregulation of chemotaxis and motility genes suggests a sophisticated plant mechanism: under N limitation, maize exudates may actively discourage the colonization of microbes that compete for scarce N resources without providing a reciprocal N benefit [77-1].

Phosphorus

Phosphorus (P) availability is another critical bottleneck constraining primary plant productivity and cellular functions [78,79]. Unlike carbon and nitrogen, P lacks a significant gaseous phase [80], with atmospheric inputs limited to minor mineral aerosol deposition [2-77]. Although P is geologically abundant in the Earth's crust, it is predominantly locked in apatite minerals, which weather too slowly to serve as a viable biological input, rendering most soils inherently deficient in plant-available phosphate [82,83]. Furthermore, existing inorganic and organic P pools are rapidly adsorbed onto soil minerals or immobilized within biomass [84]. Consequently, modern agriculture relies heavily on phosphate fertilizers derived from mined rock phosphate, a finite resource whose high-quality reserves are rapidly depleting [80]. This scarcity has intensified efforts to engineer crops with enhanced P acquisition efficiency.

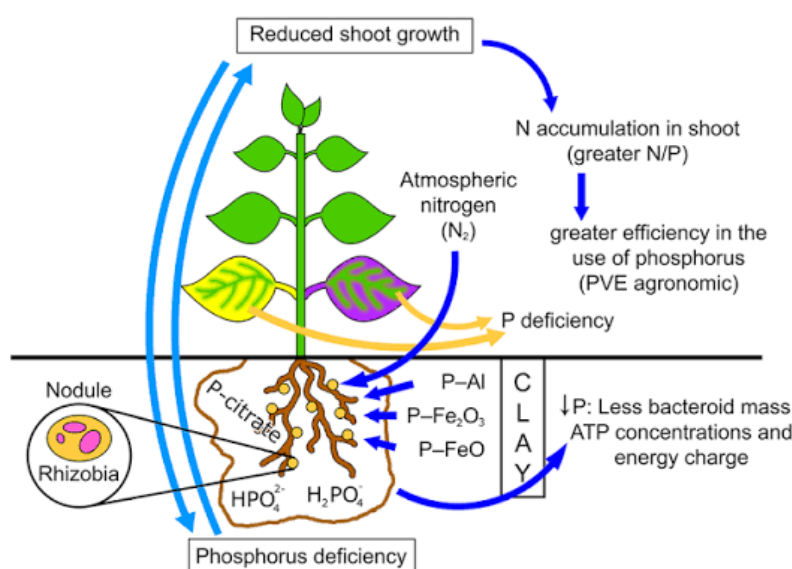


Figure 6. Phosphorus Dynamics in the Soil-Plant-Environment Relationship in Cropping Systems

Microbial communities play a dual role in P dynamics: they can solubilize immobilized P or stimulate root architecture to enhance plant uptake, yet they remain equally susceptible to P limitation and must compete directly with the host for this scarce resource [84]. Microbiome responses to P availability are highly context-dependent, ranging from modest compositional shifts in *Arabidopsis* [85] to no discernible change in switchgrass (*Panicum virgatum*) [86] and ryegrass (*Lolium perenne*) [87]. In maize, however, P fertilization significantly alters rhizosphere bacterial diversity and composition [88], with P availability acting as a stronger determinant of community structure in the rhizosphere and endosphere than plant genotype or soil compartment [89]. Under low P conditions, selective pressures enrich for P-solubilizing bacteria in the rhizospheres of ryegrass and clover (*Trifolium repens*) [168], and increase the diversity of bacteria harboring alkaline phosphomonoesterase genes—critical for mineralizing organic P—in barley, though this response was notably absent in wheat [90,91]. These disparities highlight the species-specific nature of root-microbiome interactions under P stress [92]. To cope with ubiquitous P deficiency, plants have evolved sophisticated Phosphate Starvation Responses (PSRs). These include architectural modifications, such as enhanced lateral root branching and root hair proliferation, to forage for P in topsoil layers [94,95], the upregulation of high-affinity P transporters [96], and the exudation of phosphatases and organic acids to mobilize sorbed P (Figure 1) [97,98]. For instance, P-deficiency triggers the exudation of amino acids in pine (*Pinus radiata*) [99], common bean [100], and rice. Ultimately, this orchestrated exudative remodeling under low P conditions is strongly linked to improved P acquisition, as demonstrated in maize and mung bean (*Vigna radiata*) [101].

Conclusions

The soil microbiome—comprising highly dynamic networks of bacteria, archaea, fungi, and viruses—acts as the primary engine driving global biogeochemical cycles and underpinning ecosystem resilience. However, compounding climate change drivers, including elevated CO₂, warming, drought, and flooding, are fundamentally rewiring these subterranean communities. This restructuring is characterized by a shift in the balance between fast-growing r-strategists and stress-tolerant K-strategists, which directly governs the critical trade-off between organic carbon mineralization and stabilization. Consequently, these microbial demographic shifts dictate whether soils function as net carbon sources or sinks, while simultaneously modulating the emission of potent greenhouse gases such as N₂O and CH₄. Crucially, abiotic stresses profoundly alter the phyto-microbial dialogue. Stress-induced remodeling of root exudation profiles—such as the release of terpenoids under nitrogen limitation or organic acids during phosphate starvation—selectively recruits beneficial plant growth-promoting microorganisms (PGPMs). Through mechanisms like ACC deaminase production and enhanced nutrient solubilization, these targeted microbial assemblages confer critical stress mitigation to host plants, highlighting a promising, yet underutilized, avenue for agricultural adaptation. Translating this fine-scale microbial ecology into actionable climate solutions, however, remains a formidable challenge. A primary bottleneck is the persistent disconnect between micro-scale mechanistic insights—derived from metagenomics and trait-based frameworks—and the macro-scale resolution required for Earth system climate models. While engineering and applying targeted bioinoculants presents a viable strategy to enhance crop resilience and soil carbon sequestration, microbial interventions alone are inherently insufficient to offset the unprecedented scale of ongoing soil degradation and greenhouse gas emissions. Instead, a paradigm shift towards integrated sustainable land management is urgently required. Such an approach must synergize microbial strategies with optimal agronomic practices to sustain plant productivity, regulate water dynamics, conserve biodiversity, and maximize carbon sequestration. Ultimately, safeguarding these fragile subterranean ecosystems demands not only the advancement of predictive, trait-based microbiome modeling, but also unwavering political will and a globally coordinated effort to curtail the anthropogenic greenhouse gas emissions that are the root cause of the climate crisis.

Conflict of interest. Nil

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