



Reviews and syntheses: Microbial Carbon Fixation in Dryland: A component of Global Carbon Cycle

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Abstract. Atmospheric carbon dioxide (CO₂) sequestration is commonly attributed to plant-driven processes, while the contribution of soil microorganisms remains comparatively underexplored. This imbalance is particularly relevant in dryland ecosystems, which cover over 45% of Earth's land surface and store a substantial fraction of global soil organic carbon. Despite their vast extent and ecological significance, current frameworks often overlook the metabolic potential of microbial communities inhabiting these environments. In drylands, microorganisms have evolved diverse metabolic strategies to capture and store atmospheric carbon, supported by multiple carbon-fixation pathways that extend beyond the Calvin–Benson–Bassham cycle. Here, we examine microbial carbon fixation in dryland ecosystems as an underexplored component of the global carbon cycle. We highlight the diversity, metabolic flexibility, and stress adaptations of carbon-fixing microbes and discuss the dominant pathways supporting carbon assimilation under arid conditions. By integrating evidence across studies, the findings suggest that microbial processes in drylands can contribute to carbon sequestration in ways not fully captured by plant-centered perspectives. This review provides a framework for incorporating microbial metabolic diversity into current models of terrestrial carbon cycling and highlights its relevance for climate change mitigation strategies.

25 1. Introduction

Soil represents the largest terrestrial carbon pool and plays a critical role in global climate mitigation. Dryland ecosystems, which cover >45% of Earth's land surface, contribute substantially to global carbon storage, with their overall impact driven largely by their vast spatial extent (Moharana et al., 2024). Reduced decomposition rates under arid conditions further enhance long-term carbon retention, reinforcing the importance of aridity in the global carbon balance (Wu et al., 2024). Current investigations of terrestrial carbon sequestration have largely focused on plant-driven processes. However, this perspective may overlook the contribution of soil microbial communities, particularly in ecosystems where vegetation is sparse or



intermittent (Schimel, 2018). In drylands, where plant productivity is often limited, microorganisms may play a more prominent role in carbon fixation than typically recognized (Wei et al., 2023).

Microbial carbon fixation in drylands is supported by a diverse range of metabolic pathways, allowing
35 microorganisms to assimilate carbon under fluctuating and extreme environmental conditions. In addition to classical autotrophic processes, many soil microbes can utilize alternative energy sources, such as atmospheric trace gases, to sustain carbon assimilation (Leung et al., 2020). These adaptive strategies may enable microbial communities to contribute to carbon sequestration in ways not fully captured by current models of terrestrial carbon cycling.

Despite growing interest in soil carbon dynamics, the role of microbial metabolism in dryland carbon sequestration remains
40 insufficiently integrated into current research. This gap is particularly relevant given the global distribution of drylands and the vast diversity of microbial communities inhabiting these environments.

In this study, we examined microbial carbon fixation in dryland ecosystems as an underexplored component of the global carbon cycle. We synthesize recent advances in microbial ecology and metabolism, highlight dominant carbon-fixation pathways, and discuss how microbial processes may influence carbon sequestration under arid conditions. By integrating these
45 perspectives, we aimed to provide a more comprehensive understanding of carbon dynamics in drylands and identify key directions for future research.

2. Dryland Microbial Contribution to Carbon Fixation

Microbial communities are key contributors to carbon cycling in dryland ecosystems, where plant primary productivity is often
50 limited (Maestre et al., 2021). Although traditionally considered secondary to plant-driven processes, autotrophic microorganisms account for approximately 4% of global annual CO₂ fixation (Bossio et al., 2020), demonstrating a measurable contribution to carbon capture at the global scale.

Reported fixation rates average approximately 22 mg C m⁻² day⁻¹ (Lynn et al., 2017), and when considered across the extensive global coverage of drylands, these rates translate into a substantial cumulative contribution to terrestrial carbon
55 sequestration. In addition, soil microbial biomass (MBC) stores approximately 23.2 Pg of carbon in the top 1 m (0–100 cm) of soil, reinforcing the role of microorganisms as a significant, yet often underrecognized, carbon reservoir (León-Sobrino and 2019).

The composition of dryland microbial communities further supports their functional importance. Bacteria dominate these systems (≈93%), followed by fungi (6%) and archaea (0.43%), reflecting adaptation to diverse energy sources that sustain
60 carbon cycling under resource-limited conditions (León-Sobrino et al., 2019). Among these groups, *Actinomycetota* are particularly abundant due to their metabolic versatility, capacity for sporulation, and ability to conserve energy by suppressing costly processes such as motility and macromolecule synthesis (van Bergeijk et al., 2020). Other microbial taxa, including *Pseudomonadota*, *Cyanobacteria*, *Bacteroidota*, *Firmicutes*, *Gemmatimonadota*, *Nitrospirota*, and *Thaumarchaeota*, also contribute to nutrient cycling and broader biogeochemical processes (Bukar et al., 2019; Zhang et al., 2023).



65 Microbial carbon fixation in drylands is supported by a wide range of metabolic strategies that enable carbon assimilation under fluctuating and extreme environmental conditions. In contrast to plant-driven processes, microbial activity is not strictly constrained by phenology; instead, it is primarily regulated by abiotic factors such as soil temperature, moisture, pH, organic carbon content, and precipitation (Zheng et al., 2022). This flexibility allows microbial communities to rapidly respond to transient resource availability, particularly following precipitation events.

70 Biological soil crusts (BSCs) are important contributors to carbon fixation in many dryland systems and function as key primary producers in environments with limited vegetation (Xu et al., 2022). However, carbon fixation is not restricted to these surface-associated communities. Free-living soil microorganisms also contribute significantly to atmospheric CO₂ assimilation across diverse dryland soil types (Ge et al., 2013; Zhao et al., 2018). Together, these findings indicate that microbial carbon fixation extends beyond localized niches and represents a widespread process across dryland ecosystems.

75 Quantitative assessments further support the significance of microbial contributions. Microbial gross primary productivity (GPP) in drylands has been estimated to reach approximately 18.2% of plant GPP (Chen et al., 2021a), highlighting the need to incorporate microbial processes into terrestrial carbon budgets. Conventional satellite-based approaches that focus exclusively on vegetation may therefore underestimate total GPP in drylands by neglecting microbial activity.

80 The persistence of microbial carbon fixation under harsh dryland conditions is enabled by a suite of adaptive strategies. Microorganisms can alternate between active growth and dormancy, accumulate compatible solutes for osmotic balance, produce extracellular polymeric substances to retain moisture, and stabilize cellular components under stress (Lebre et al., 2017). In addition, the presence of genes associated with carbon fixation (e.g., *cbbL*) and energy-efficient metabolic pathways supports rapid reactivation following environmental changes (Zhao et al., 2018).

85 Microbial autotrophy in drylands is fueled by phototrophic and chemolithoautotrophic processes. Oxygenic phototrophs, such as *Cyanobacteria*, contribute significantly to energy capture and carbon assimilation, while chemolithoautotrophic microorganisms utilize inorganic compounds such as CO, H₂, sulfate, phosphite, and iron as energy sources (Correa et al., 2023). In arid and hyper-arid environments, chemolithoautotrophy may play a particularly important role due to its metabolic versatility and capacity to operate under extreme conditions (Pinheiro et al., 2023). Higher expression
90 of chemoautotrophic carbon-fixation genes relative to photosynthetic genes further supports this functional shift (León-Sobrino et al., 2019).

Evidence from *in situ* carbon tracing and metagenomic analyses indicates that a substantial proportion of CO₂ fixation genes in dryland soils are associated with chemoautotrophic and heterotrophic microorganisms (Liu et al., 2021). These findings reinforce the importance of incorporating microbial metabolic diversity into current representations of terrestrial
95 carbon cycling.

Collectively, these results demonstrate that microbial carbon fixation in drylands is not a marginal process but a widespread and functionally significant component of the global carbon cycle. Integrating microbial contributions into carbon-



cycle models will improve estimates of carbon fluxes and enhance predictions of soil carbon sequestration potential under ongoing climate change, particularly in expanding dryland regions.

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3. Distribution of Carbon-Fixation Pathways in Dryland

Autotrophic microorganisms employ a diverse set of carbon-fixation pathways, reflecting the evolutionary and ecological constraints that shape carbon assimilation across environments. Seven major pathways have been described, including the Calvin–Benson–Bassham (CBB) cycle, the reductive tricarboxylic acid (rTCA) cycle, the reductive acetyl-CoA (Wood–Ljungdahl, WL) pathway, and some variants of the 3-hydroxypropionate (3-HP) and hydroxybutyrate cycles (Berg et al., 2011; Figueroa et al., 2018; Correa et al., 2023). In addition to these established pathways, other natural C-fixation cycles have been described in some bacteria, and analyzed by combining large-scale omics and biochemistry, such as the reductive hexulose-phosphate (RHP) cycle and reverse oxidative tricarboxylic acid cycle (roTCA) (Garritano et al., 2022) (Table 1). This metabolic diversity provides microorganisms with the flexibility to sustain carbon fixation under a wide range of environmental conditions.

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The distribution of these pathways is strongly influenced by environmental constraints, particularly energy availability and oxygen levels. Early metabolic networks likely combined elements of the rTCA and WL pathways, conferring robustness under fluctuating conditions despite relatively low energy efficiency (Braakman and Smith, 2012). As atmospheric oxygen levels increased, selective pressures favored pathways that were more tolerant of oxidative stress, driving the diversification of modern carbon-fixation strategies (Zhao et al., 2020). Adaptations such as the evolution of carboxysomes in certain chemolithoautotrophs further enhance carbon assimilation efficiency by minimizing carbon loss and protecting oxygen-sensitive enzymes (Correa et al., 2024).

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In dryland ecosystems, these environmental constraints are particularly pronounced. Low nutrient availability, limited water, and fluctuating oxygen conditions favor energy-efficient metabolic strategies, resulting in a distinct distribution of carbon-fixation pathways compared with more productive ecosystems. Although the CBB cycle dominates carbon fixation in many terrestrial environments, alternative pathways, particularly the rTCA cycle and WL pathway, are more prevalent in oligotrophic dryland soils (Liu et al., 2018).

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The predominance of the rTCA cycle in drylands reflects its relatively low energy requirement and suitability for microaerophilic conditions. This pathway operates in the reverse direction of the oxidative tricarboxylic acid cycle, producing acetyl-CoA from CO₂ with lower ATP demand than the CBB cycle (Hügler and Sievert, 2011). Its reliance on oxygen-sensitive enzymes further explains its association with low-oxygen microenvironments commonly found in dryland soils. Following the rTCA cycle, the DC/HB cycle and WL pathway also contribute significantly, likely due to their high energy efficiency and adaptability to nutrient-limited conditions (Yang et al., 2024).

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Empirical evidence supports the ecological relevance of these pathways in drylands. Metagenomic analyses have revealed a high abundance of genes associated with the rTCA cycle, often exceeding those of the CBB and other pathways (Liu et al., 2018). Stable isotope labeling studies further demonstrate that carbon fixation in dryland soils is closely linked to

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the activity of multiple pathways, including the rTCA, 3-HP, and WL pathways (Liu et al., 2018). These findings indicate that microbial carbon fixation in drylands relies on a network of complementary metabolic routes rather than a single dominant pathway.

135 Environmental gradients, particularly precipitation, play a central role in shaping pathway distribution. The abundance of carbon-fixation genes generally increases with moisture availability, with semi-humid regions supporting greater pathway diversity and activity than more arid sites (Huang et al., 2022). These findings suggest that water availability acts as a primary regulator of microbial carbon fixation, influencing both the abundance and activity of autotrophic communities.

140 Although alternative pathways dominate in many dryland soils, the CBB cycle remains important in specific microenvironments. For example, BSCs often exhibit high *cbbL* gene abundance, reflecting the contribution of phototrophic microorganisms such as *Cyanobacteria* (Zhao et al., 2021). In these localized niches, carbon fixation is driven primarily by light-dependent processes, highlighting the spatial heterogeneity of metabolic strategies within dryland ecosystems.

145 Beyond phototrophy, chemolithoautotrophic processes play a critical role in sustaining carbon fixation under extreme conditions. These microorganisms utilize inorganic compounds such as CO, H₂, and reduced sulfur or iron species as energy sources, enabling carbon assimilation independent of light availability (Correa et al., 2023). In arid and hyper-arid environments, chemolithoautotrophy may be particularly important due to its capacity to operate under severe resource limitations (Pinheiro et al., 2023).

150 Emerging evidence also highlights the potential role of thermophilic microorganisms in dryland carbon cycling. These organisms possess heat-stable enzymes and metabolic adaptations that enable activity at elevated temperatures, which are increasingly prevalent in expanding drylands (Schultz et al., 2024). Although their roles in carbon mineralization are well established, their contribution to CO₂ fixation remains poorly understood, representing an important avenue for future research.

155 Collectively, these findings demonstrate that the distribution of carbon-fixation pathways in drylands is shaped by strong environmental constraints that favor metabolic efficiency and flexibility. The predominance of alternative pathways over the CBB cycle highlights the importance of considering microbial metabolic diversity when assessing carbon sequestration in these ecosystems. Integrating these processes into current models of terrestrial carbon cycling is essential for accurately understanding carbon fluxes in drylands and improving predictions under ongoing climate change.

4. Carbon Cycle Dynamics in Drylands

160 Understanding carbon cycling in drylands is essential for contextualizing the role of microbial processes within the broader carbon system. Carbon fluxes in dryland ecosystems play a critical role in the global carbon cycle by mediating exchanges between the atmosphere, soil, and biosphere through abiotic and biotic processes. Although terrestrial ecosystems exchange more CO₂ with the atmosphere than oceans, soils alone store >2,300 Pg of carbon in the top three meters (Regnier et al., 2022), highlighting their importance as long-term carbon reservoirs.

165 In drylands, carbon cycling is characterized by a distinctive balance between soil organic carbon (SOC) and soil inorganic carbon (SIC). Unlike more productive ecosystems, in which SOC dominates, dryland carbon stocks are largely



governed by SIC pools, which exhibit long geological residence times and serve as major carbon reservoirs (Moharana et al., 2021). The formation and stabilization of SIC are primarily driven by abiotic processes such as carbonate weathering and bicarbonate leaching; however, increasing evidence suggests that microbial activity also contributes to inorganic carbon formation in desert soils (Liu et al., 2020).

170 Despite the dominance of SIC, SOC remains a critical and dynamic component of dryland carbon cycling. SOC is typically concentrated beneath vegetation and within subsoil layers, where it exhibits greater stability and longer residence times compared to surface carbon (Shi et al., 2020). Its persistence reflects the balance between carbon inputs through photosynthesis and outputs through microbial respiration and decomposition. In this context, microbial processes play a central role in regulating SOC dynamics by mediating carbon stabilization and mineralization.

175 Microbial activity also governs key processes such as the priming effect, which determines whether soils act as net carbon sources or sinks. The addition of labile substrates can stimulate microbial decomposition of native SOC, enhancing CO₂ release, particularly in carbon-poor soils (Guenet et al., 2018). Conversely, negative priming may occur when substrate inputs reduce microbial turnover, promoting carbon retention (Chen et al., 2021b). These contrasting responses highlight the complexity of microbially mediated carbon dynamics in drylands.

180 Beyond organic carbon processes, microorganisms also influence carbon cycling through the oxidation of atmospheric trace gases. Soil microbes possessing specialized metalloenzymes consume reduced gases such as H₂ and CO, contributing significantly to global atmospheric budgets (Bay et al., 2021). These processes provide alternative energy sources that sustain microbial metabolism and indirectly support carbon assimilation under resource-limited conditions.

185 Environmental pressures further shape carbon cycling in drylands. High temperatures, low precipitation, land degradation, and soil erosion collectively reduce carbon stocks and disrupt ecosystem function (Plaza-Bonilla et al., 2015). Anthropogenic mismanagement has led to substantial carbon losses, estimated at 13–24 Pg across dryland regions (Okolo et al., 2023). Erosion removes surface SOC and enhances carbon release through mineralization and exposure of carbonate-rich substrates, accelerating carbon flux to the atmosphere.

190 Collectively, these processes demonstrate that carbon cycling in drylands is governed by a complex interplay of abiotic and biotic factors, with microbial activity acting as a key regulator of organic and inorganic carbon pools. Incorporating microbial processes into current models of dryland carbon dynamics is essential for accurately quantifying carbon fluxes and predicting ecosystem responses to climate change.

5. Biological Strategies and Systems to Enhance Carbon Fixation in Drylands

195 Enhancing carbon sequestration in dryland ecosystems requires strategies that integrate microbial processes, vegetation dynamics, and soil management. Whereas plant-based approaches have traditionally dominated carbon sequestration efforts, growing evidence indicates that leveraging microbial metabolism and plant–microbe interactions can substantially improve the efficiency of carbon fixation in these systems.



In the subsequent sections, we outline key biological strategies that can enhance carbon sequestration in drylands, emphasizing their underlying mechanisms and potential for large-scale application.

5.1. Microbial inoculants

Microbial inoculation represents a promising strategy to enhance carbon fixation in drylands by directly manipulating soil microbiomes. Functional groups such as arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria, nitrogen-fixing bacteria, and *Actinomycetota* improve nutrient cycling, soil structure, and plant resilience, thereby supporting increased carbon sequestration (Kheirfam, 2020; Coleine et al., 2024).

Empirical evidence demonstrates that microbial inoculants can enhance short- and long-term carbon storage. Short-term gains arise from increased microbial biomass and carbon-fixation activity, whereas long-term sequestration is promoted through improved vegetation establishment and stress tolerance (Maestre et al., 2021; Fadji et al., 2022). *Cyanobacteria* are particularly effective due to their rapid growth, tolerance to extreme conditions, and capacity to contribute to biological soil crust formation. Quantitative studies further highlight their potential: co-inoculation of *Cyanobacteria* (e.g., *Oscillatoria* sp. and *Nostoc* sp.) with heterotrophic bacteria significantly increases carbon-fixation rates, demonstrating measurable gains in carbon sequestration at the ecosystem scale (Kheirfam, 2020).

In addition to classical autotrophic processes, some dryland microorganisms sustain activity through trace gas oxidation, maintaining metabolic readiness under prolonged drought. This strategy enables rapid reactivation following precipitation events, thereby supporting continuous contributions to carbon fixation over time (Leung et al., 2024). Microbial mediated carbonate formation also represents a potential pathway to enhance inorganic carbon storage. Approaches such as inoculation with carbonate-forming microorganisms, optimization of soil moisture and mineral availability, and promotion of biological soil crust development may increase SIC accumulation and long-term carbon retention. These findings indicate that microbial inoculation offers a scalable and mechanistically grounded approach for enhancing carbon sequestration in drylands, although further research is needed to optimize microbial consortia and ensure long-term stability across diverse environments.

5.2 Native plant species and afforestation

Vegetation plays a central role in carbon sequestration through aboveground biomass production and its influence on soil carbon inputs and plant-microbe interactions. Native and drought-adapted species are particularly effective due to their ability to allocate carbon to deep root systems, where carbon is more stable and less susceptible to decomposition (Tariq et al., 2024).

The use of native species in restoration and afforestation programs enhances carbon storage and ecosystem resilience. These plants improve soil structure, promote microbial activity, and create localized zones of enhanced biological activity even under extreme conditions (Ménard et al., 2023).

Large-scale afforestation initiatives, including programs in China, the African Sahel, and Australia, demonstrate the global commitment to vegetation-based climate mitigation strategies. Model-based projections suggest that dryland afforestation could contribute substantially to carbon sequestration, with estimated mitigation potential exceeding 50 Gt C under optimized



conditions (Rohatyn et al., 2022). However, these strategies must be carefully implemented to avoid unintended tradeoffs, particularly related to water availability and soil salinization. Optimizing species selection, spatial distribution, and ecosystem carrying capacity is essential to ensure long-term sustainability (Yang et al., 2023). Integrating plant-based approaches with microbial processes may further enhance carbon sequestration by strengthening plant–microbe interactions and improving nutrient cycling efficiency.

5.3. Biochar amendments

Biochar application represents an additional strategy to enhance carbon sequestration by simultaneously improving soil properties and microbial activity. As a stable, carbon-rich material, biochar increases SOC, enhances water retention, and improves nutrient availability in dryland soils (Brtnicky et al., 2021).

Biochar also modifies the soil microbiome by providing physical habitat, retaining moisture, and promoting microbial diversity. Increased abundance of beneficial taxa such as *Bacillus* and *Pseudomonas* has been associated with improved soil health and plant growth, while reductions in pathogenic fungi contribute to ecosystem stability (Li et al., 2020; Ajema, 2018). Changes in microbial community structure following biochar application further support its role in carbon sequestration. Enhanced microbial activity and diversity increase the efficiency of carbon cycling and stabilization processes, particularly in the topsoil layer where biological activity is concentrated (Lv et al., 2022). By simultaneously influencing physical, chemical, and biological processes, biochar provides a multifunctional approach for improving carbon storage in drylands and represents a promising tool for climate change mitigation in these environments.

6. Final Remarks

Dryland ecosystems are expanding rapidly under ongoing climate change, with increasing aridity and land degradation threatening their capacity to store carbon. Although these systems have traditionally been viewed as carbon-poor and biologically constrained, this perspective fails to fully capture the functional role of microbial communities in regulating carbon dynamics.

Throughout this review, we demonstrate that microorganisms in drylands are active contributors to carbon fixation and storage. Their metabolic diversity, capacity to operate under extreme conditions, and use of multiple carbon-fixing pathways enable carbon assimilation in environments where plant productivity is limited. These findings suggest that microbial processes represent an underappreciated component of the global carbon cycle.

Despite this, current models and policy frameworks remain largely centered on plant-driven carbon sequestration, often overlooking microbial contributions. Integrating microbial metabolism into carbon-cycle models is therefore essential to improve predictions of carbon fluxes and better represent dryland ecosystems in climate projections. From an applied perspective, strategies that combine microbial inoculation, plant-based restoration, and soil amendments offer promising avenues to enhance carbon sequestration in drylands. However, the long-term effectiveness and scalability of these approaches remain insufficiently explored across diverse dryland environments.



270 Future research should prioritize the quantification of microbial carbon-fixation rates at ecosystem scales and the integration of molecular tools, such as metagenomics and isotopic tracing, to directly link microbial activity with carbon sequestration outcomes. Expanding experimental frameworks to include microbial responses under changing atmospheric conditions will further improve our understanding of their role in climate regulation.

Ultimately, recognizing microorganisms as active regulators of carbon cycling in drylands is critical for advancing scientific understanding and climate mitigation strategies. Incorporating microbial processes into environmental policy and land management practices will be essential to fully realize the carbon-sequestering potential of these rapidly expanding ecosystems.

275 **Author contributions**

SSC: Conceptualization, methodology, writing – original draft, writing – review and editing. JS: Data curation, writing – original draft, writing – review and editing. BS: Review and editing. ASR: Validation, writing – review and editing. SM: Supervision and conceptualization, funding, writing – review and editing.

Competing interests

280 The authors declare no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

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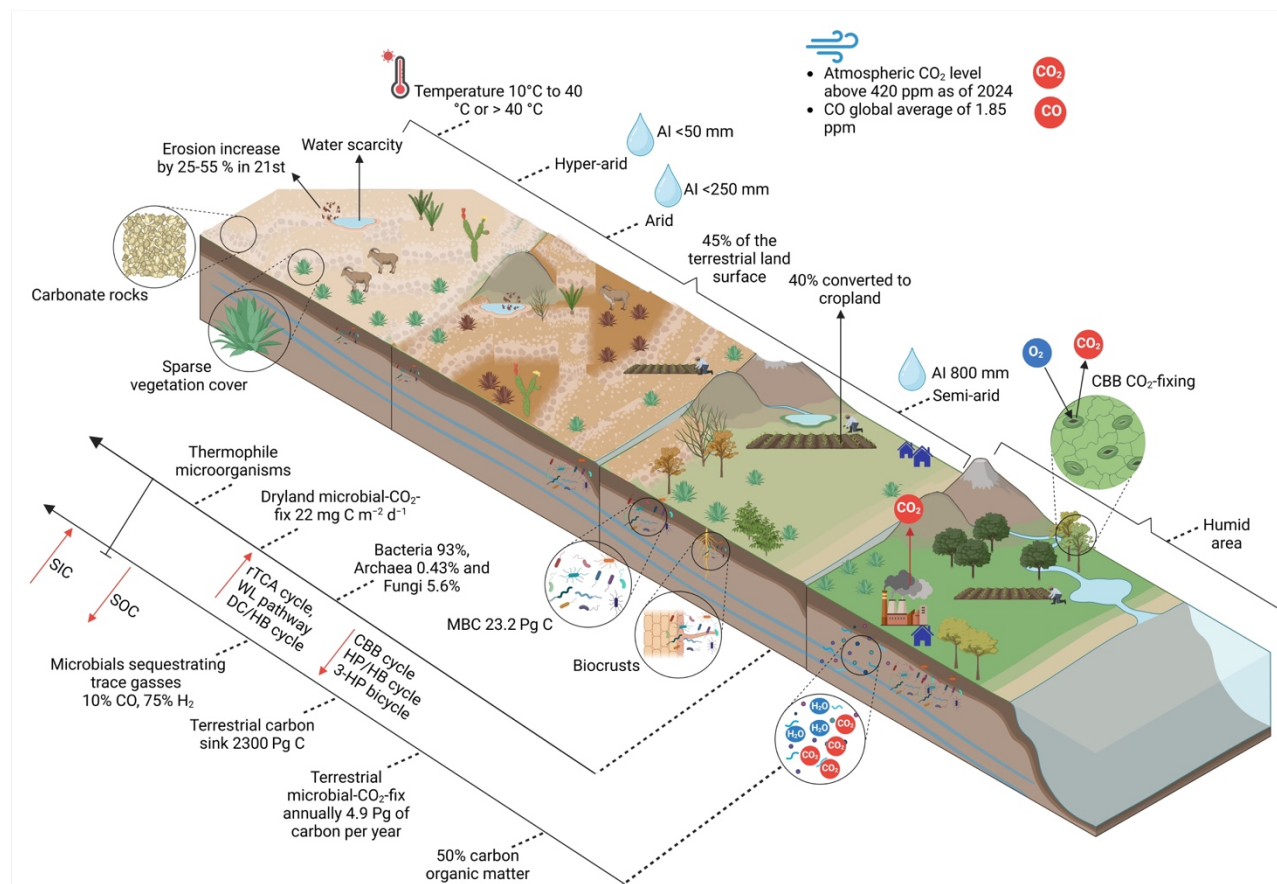
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450 Table 1. Carbon-fixation pathways and their ecological relevance in dryland environments.

Pathway	Temperature	Organisms	Energy source	Input	Output	Reductant	Key enzymes	O ₂ sensitive	Reference
Calvin–Benson	<75°C	Plants, algae, <i>Cyanobacteria</i> , aerobic <i>Proteobacteria</i> , purple bacteria, Green sulfur bacteria,	Light	3 CO ₂ , 9 ATP, 6 NAD(P)H	Glyceraldehyde-3-phosphate	NAD(P)H	RuBisCO	No	Berg and others 2011
Reductive tricarboxylic acid	<95°C	<i>Proteobacteria</i> , <i>Aquificae</i> , <i>Nitrospirae</i> , <i>Acetogenic</i> , methanogenic Archaea,	Light and sulfur	2 CO ₂ , 2 ATP, 4 NAD(P)H	Pyruvate	NAD(P)H and ferredoxin	2-Oxoglutarate synthase, isocitrate dehydrogenase	Yes	Nunoura and others 2018
Wood–Ljungdahl	<80°C	<i>Planctomycetes</i> , sulfate, <i>Archaeoglobales</i>	H ₂	2 CO ₂ , 1 ATP, 4 NAD(P)H	Acetyl-CoA	Ferredoxin	NAD-independent formate dehydrogenase, acetyl-CoA synthase-CO dehydrogenase	Yes	Berg and others 2011
3-Hydroxypropionate	<75°C	<i>Chloroflexaceae</i>	Light	3 HCO ₃ ⁻ , 5 ATP, 5 AD(P)H	Pyruvate	NAD(P)H	Acetyl-CoA carboxylase, propionyl-CoA carboxylase	No	Berg and others 2011
3-Hydroxypropionate/4-hydroxybutyrate	<73°C	Aerobic <i>Sulfobacterales</i>	H ₂ and sulfur	2 HCO ₃ ⁻ , 4 ATP, 4 NAD(P)H	Acetyl-CoA	NAD(P)H	Acetyl-CoA-propionyl-CoA carboxylase,	No	Berg and others 2011
Dicarboxylate/4-hydroxybutyrate	<98°C	Anaerobic <i>Thermoproteales</i> , <i>Desulfurococcales</i>	H ₂ and sulfur	1 CO ₂ , 1 HCO ₃ ⁻ , 3 ATP, 4 NAD(P)H	Acetyl-CoA	NAD(P)H and ferredoxin	Pyruvate synthase, PEP carboxylase	Yes	Berg and others 2011
Reductive hexulose-phosphate	<30°C	<i>Methanospirillum hungatei</i>	H ₂	CO ₂ , 3 ATP, 2 NAD(P)H	Gluconogenesis and glycolysis	NAD(P)H	RuBisCO	No	Kono and others 2017
Natural reductive glycine	<30°C	<i>Candidatus Phosphitovorax anaerolimi</i> , <i>Desulfovibrio desulfuricans</i>	Phosphate	CO ₂ , ATP, NAD(P)H	Formate/pyruvate	NAD(P)H and ferredoxin	CO ₂ -reducing formate dehydrogenase (fdhAB)	-	Figuroa and others 2018
Reverse oxidative citric acid cycle	<78°C	<i>Desulfurella acetivorans</i>	H ₂	CO ₂ , ATP, NAD(P)H	Acetyl-CoA	Ferredoxin	Citrate synthase	-	Mall and others 2018



Fig. 1: Spatial distribution of microbial carbon fixation across a terrestrial gradient. The figure highlights the central role of dryland microorganisms in carbon fixation and sequestration, where they represent dominant carbon-fixing agents. In arid and semi-arid regions, microorganisms drive carbon fixation through alternative pathways such as the rTCA cycle, WL pathway, and DC/HB cycle. In humid regions, carbon fixation is mainly driven by the CBB cycle, associated with plant-dominated systems.



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