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Soil Carbon Pool as Influenced by Soil Microbial Activity—An Overview

Goutham Thotakuri[1], Srushtideep Angidi[2*], Akshara Athelly[3]

[1]Department of Plant Soil and Microbial Sciences, Michigan State University, East Lansing, MI, USA
[2]Department of Plant Pathology, North Dakota State University, Fargo, ND, USA
[3]Agricultural and Biological Engineering Department, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, FL, USA
Email: *srushtideep.angidi@ndsu.edu

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Abstract

Soil is a significant carbon reservoir with the capacity to store carbon twice as much as the atmosphere or plants. Given the significant potential of soil to capture and store atmospheric CO_2, it presents a viable solution for mitigating the present and future impacts of climate change. However, due to its high susceptibility to global environmental issues like land degradation, loss of biodiversity, and climate change, monitoring and protecting soil carbon pools is a complex challenge. Intensive agricultural operations have detrimental effects on the soil, including the rapid breakdown of soil organic carbon, which releases excess carbon into the air, causing increased atmospheric CO_2 levels and a depletion of the soil carbon reserves. The diversity and abundance of soil microbial communities play a crucial role in controlling essential ecosystem processes, including the decomposition of organic matter and nutrient cycling, including carbon. Heterotrophic soil microorganisms facilitate the soil organic matter turnover to obtain the nutrients and energy required for their growth and maintenance. Therefore, the microbial residues and exudates have up to 80% carbon in the stable soil organic matter fractions. This overview attempts to summarize the information on various carbon pools, soil carbon interaction with microbes, impacts on environmental changes, and strategies to enhance the storage of belowground carbon.

Keywords

Soil Carbon, Microorganisms, Decomposition, Carbon Storage, and Land-Use Management

1. Introduction

Soil carbon dynamics are influenced by a myriad of factors, among which soil microorganisms play a central role. Although often unseen, these microorganisms wield significant influence, orchestrating complex processes that govern carbon cycling within terrestrial ecosystems. In this review, we explore the symbiotic relationship between soil microorganisms and the soil carbon pool and how microbial communities actively drive carbon sequestration and decomposition, thus impacting the health and function of ecosystems.

The interaction between soil microorganisms and organic matter lies at the core of comprehending soil carbon dynamics. These microorganisms, including bacteria, fungi, archaea, and other microscopic life forms, act as primary decomposers of organic materials. Enzymatic processes break down complex carbon compounds into simpler forms, releasing carbon dioxide (CO_2) into the atmosphere—a crucial step in the carbon cycle.

However, soil microorganisms also play a significant role in stabilizing and sequestering carbon. They contribute to forming stable organic carbon pools in the soil by forming microbial biomass and producing extracellular substances such as glomalin and humic substances. Moreover, microbial activities promote soil aggregation, offering physical protection to organic matter against decomposition. The diversity and composition of soil microbial communities profoundly affect carbon turnover rates and soil carbon storage. Different microbial groups possess distinct metabolic capabilities and substrate preferences, influencing the efficiency of carbon decomposition and stabilization. Changes in microbial community composition, driven by environmental factors like soil moisture, temperature, and nutrient availability, can significantly alter carbon cycling processes.

Furthermore, microbial interactions with plant roots further influence soil carbon dynamics. Mycorrhizal fungi facilitate nutrient uptake and carbon allocation to the soil through rhizodeposition in mutualistic associations with plant roots. This underground input of carbon fuels microbial activity and fosters soil organic matter formation, contributing to long-term carbon sequestration. This overview focuses on the diverse roles of soil microorganisms in shaping the soil carbon pool. By synthesizing current research findings and elucidating microbial mechanisms involved in carbon cycling, we aim to deepen our understanding of soil carbon dynamics and provide insights for sustainable soil management and carbon sequestration strategies.

2. Soil Carbon Pool

The balance between photosynthesis and respiration dominates the global carbon cycle. Photosynthesis is a single-step function, whereas respiration involves a variety of processes. Slight disparities can contribute to considerable interannual fluctuation in atmospheric CO_2. Carbon is transported from the atmosphere to soil by autotrophic organisms that synthesize atmospheric carbon dioxide into organic material, primarily photosynthesizing plants, and photo- and chemoautotrophic microorganisms. Carbon that is fixed is subsequently returned to the atmosphere through several routes that account for autotrophic and heterotrophic species respiration. Decomposition of organic material by organic carbon-consuming heterotrophic bacteria uses carbon from either plant, animal, or microbial origin as a metabolic substrate for metabolism, keeping some carbon in their biomass while releasing the remainder as metabolites or CO_2 back into the atmosphere. To achieve their primary objective of survival through reproduction, soil microorganisms move carbon across environmental compartments. As a result, microbes use various organic and inorganic carbon forms as carbon and energy sources (Gougoulias et al., 2014).

A single plant root is home to a wide variety of microbes, including bacteria and fungi. Plant underground production is frequently equal to, if not greater, aboveground plants (McCulley et al., 2005). The roots of many kinds of grass, shrubs, and tree roots grow to 1 m or even deeper (Craine et al., 2003). Decomposer organisms specialize in specific microhabitats and C pools (Kögel-Knabner et al., 2008). According to Poll et al. (2008), bacteria and fungi display various resource-use methods. Fungi directly absorb substrates from the litter layer, whereas bacteria absorb substrates from the soil under the litter layer. Microbial mineralization is the primary cause of soil organic matter degradation; thus, it is critical to research microbial degradation ecology in agricultural contexts where management and edaphic variables influence microbial activity and, as a result, the turnover rates of soil organic pools (Schjønning et al., 2004).

Several biotic and abiotic elements are responsible for the influence of microbial diversity and biomass in the soil. Furthermore, there is an increasing interest in comprehending the impact on soil microbial diversity and biomass (Bastida et al., 2021). Carbon trading brings the storage capacity and quantification of carbon in soils into the picture (Serrano et al., 2016).

3. Soil Microbiome

Soil, often overlooked, harbors a vast and diverse microbial community, with billions of microorganisms present per gram of soil. This microbial diversity encompasses various taxa, including bacteria, fungi, archaea, and other microscopic organisms, each adapted to thrive in different soil environments (Delgado-Baquerizo et al., 2018; Fierer & Jackson, 2006). The composition and abundance of soil microorganisms are influenced by factors like soil type, pH, moisture content, temperature, and organic matter content (Fierer & Jackson, 2006; Lauber et al., 2008). Microbial communities form intricate networks of interactions that drive essential ecosystem processes, including nutrient cycling, carbon dynamics, and plant-microbe interactions (DeAngelis et al., 2009; Philippot et al., 2010).

Soil microorganisms play a crucial role in carbon cycling, mediating the decomposition of organic matter and the stabilization of soil carbon pools (Schimel & Schaeffer, 2012). Through enzymatic processes, microorganisms break down complex carbon compounds in organic matter, releasing CO_2 into the atmosphere as a byproduct (Spaccini et al., 2002). Microbial activities also contribute to carbon sequestration by forming microbial biomass and synthesizing organic compounds, which can be stabilized in soil aggregates (Six et al., 2000). The microbial decomposition of organic matter is a fundamental process in soil carbon dynamics, influencing soil fertility, nutrient availability, and greenhouse gas emissions (Fontaine et al., 2007; Wieder et al., 2013).

Microorganisms are key players in nutrient cycling, facilitating the transformation and recycling of essential nutrients such as nitrogen (N), phosphorus (P), and sulfur (S) (Falkowski et al., 2008). Soil microorganisms drive processes such as N fixation, nitrification, denitrification, and mineralization, which are critical for soil fertility and plant productivity (Singh et al., 2010). For example, nitrogen-fixing bacteria convert atmospheric nitrogen into ammonia, making it available for plant uptake, while nitrifying bacteria oxidize ammonia to nitrate, a form of N that plants can utilize (Giller et al., 1998). Microbial-mediated nutrient cycling is essential for maintaining ecosystem health and productivity, particularly in nutrient-limited environments (Cleveland & Liptzin, 2007).

Soil microorganisms form symbiotic relationships with plant roots, influencing plant nutrient uptake, disease resistance, and stress tolerance (Van Der Heijden et al., 2008). Mycorrhizal fungi, for example, establish mutualistic associations with plant roots, facilitating the exchange of nutrients (such as phosphorus) between plants and soil (Smith & Read, 2010). Additionally, rhizosphere microorganisms can produce phytohormones and secondary metabolites that enhance plant growth and defense mechanisms (Berendsen et al., 2012). Plant-microbe interactions are vital for ecosystem functioning, contributing to soil health, biodiversity, and resilience (Vandenkoornhuyse et al., 2015).

4. Interactions between Soil Microbes and SOC

Soil microbiome, with at least 25% of all species on earth, is the most diverse community in the biosphere (Sokol et al., 2022). The complex network of interactions between soil microorganisms and SOC serves as the fundamental basis for the ecosystem's functioning and the soil's overall health. Therefore, the interactions between soil microbes and SOC substantially impact the belowground carbon transfer and overall carbon cycling (Schimel & Schaeffer, 2012). The soil microbiota, which includes a wide range of bacteria, fungi, archaea, and other microorganisms, exert significant control on the development and characteristics of SOC through several mechanisms, including decomposition, mineralization and immobilization, stabilization, physical protection, aggregation, and symbiotic relationships (Ramesh et al., 2019).

4.1. Decomposition and Mineralization

Decomposition is a biological phenomenon characterized by the physical disintegration and biochemical conversion of complex organic compounds from dead material into more basic organic and inorganic compounds carried by microbes.

The major source for microbial biological activity and the carbon cycling process is continuously adding decaying plant residues to the soil surface (Khatoon et al., 2017). The primary purpose of microbes in decomposing organic material is to 1) derive energy for growth, 2) supply carbon for cellular component formation, and 3) extract other nutrients for cell growth. The enzymatic processes heavily drive organic matter decomposition. Intracellular enzymes metabolize simple compounds like monosaccharides (glucose and fructose). Extracellular enzymes are essential in breaking down polysaccharides, as the microbial cell wall is impenetrable to complex compounds. Therefore, when organic residues are added to soil, they are primarily acted upon by extracellular enzymes to be broken down into their basic components and subsequently proceeded by intracellular enzymes (Wallenstein & Burns, 2011). The availability of SOC for microbial breakdown is essential for several processes in carbon cycling as it regulates the rate of CO_2 released into the atmosphere, defines the origins of soil CO_2, impacts the microbial activity and composition, and indicates the amount of carbon stored in the soil (Bardgett et al., 2008). Soil organic carbon comprises several pools that exhibit variations in stability and availability and are distinguished by specific turnover rates. The decomposability of older, more resistant carbon pools is comparatively lower when compared to that of younger carbon pools. The soil microbes respiring retain a fraction of C into their biomass and release the rest into the soil, which is further cycled back to the atmosphere as CO_2. Mineralization, specifically, is converting the organic form of carbon into an inorganic form that plants and microbes readily absorb. Soil organic carbon mineralization results in the emission of CO_2, accounting for about 60% of total greenhouse impacts (Hossain et al., 2017). Therefore, detailed knowledge of the carbon mineralization of organic materials added to soil is vital for predicting CO_2 emissions and thus helps determine necessary management practices. When the mineralization rate exceeds organic matter input, it produces net CO_2 emissions. However, several factors discussed in the previous sections determine the mineralization rate, including the quality of residues. The portion of plant biomass added to the soil forms more stable humic substances. It contributes to various organo-mineral complexes and micro aggregates that stabilize soil carbon and promote increased carbon sequestration (Lal, 2016).

Meanwhile, the light fraction of organic matter is generally more soluble. It possesses more superficial structures than stable SOC fractions, thus making them more susceptible to microbial breakdown through enzymatic activity. Because the microbial breakdown of organic materials releases 99% of CO_2 of the total emission, the belowground soil organic pool decreases. Therefore, belowground carbon capture is the key mechanism that helps to make the soil a sink rather than a source of atmospheric CO_2.

4.2. Aggregation, Physical Protection, and Stabilization

The degree of SOM decomposition is a vital factor in developing and stabilizing the aggregate structure for SOC sequestration. Hence, the role of SOM in soil aggregation is paramount in SOC sequestration. Microbial processes acting on plant residues control the aggregation of soil particles. By breaking down fine and coarse organic residues, microbes are responsible for producing a binding material from organic materials for aggregation (Blanco-Canqui & Lal, 2004). Microbial polysaccharides stabilize macroaggregates, whereas humic substances stabilize microaggregates. The size, strength, and configuration of aggregates depend on the type of organic binding agent (temporary, transient, and persistent). Temporary agents are mostly plant roots, fungal and mycorrhizal hyphae, and algae that grow simultaneously with the plant roots and generate a visible organic skeleton to entangle the mineral particles by adsorption from macro aggregates. However, due to their larger constituents, the temporary agents are easily affected by tillage operations. Polysaccharides and organic mucilages are the primary constituents of transient agents. High molecular weight, non-humic polysaccharides are easily liberated from organic residues and break down quickly in microbial processes. Typically, 10 - 50 μm aggregates are bound together by polymer bridges made of polysaccharides, which are more easily absorbed by clay particles than fulvic or humic acids. Polysaccharides remain temporarily undecomposed while combining clay particles into macroaggregates due to their decreased immobility being negatively charged. Persistent agents comprise highly degraded organic molecules, including polymers, polyvalent cations, and humic substances. The persistent agents are crucial because they are associated with microaggregation and long-term SOC sequestration. The inability of SOC to be accessed spatially for microbial decomposition within soil aggregates is a significant factor for stability. As discussed above, the formation of soil structure is an essential mechanism that ensures physical protection. One of the critical factors for soil carbon stock in yop layers is the soil aggregates retaining at least 90% of organic carbon. The nature and characteristics of aggregates determine the accumulation pattern of SOC (Yu et al., 2015). However, the size ranges of aggregates formed have a significant role in the physical protection of SOC. Extensive studies have reported that most labile organic carbon is stored in macroaggregates (>0.25 mm) than in microaggregates (<0.25 mm), indicating the significance of soil physical structure (different aggregate size fractions) in the process of SOC cycling. For example, Wu et al. (2023) reported that soil microaggregates of 30 - 250 μm are crucial in SOC protection due to the spatial inaccessibility of organic carbon to microbes and extracellular enzymes. Similarly, Omar et al. (2023), in their study of soil respiration, concluded that aggregate-associated SOC fractions were most significant in the 50 - 250 μm size fraction. Few studies have also reported the importance of macroaggregates in SOC accumulation. The mechanism behind the SOC accumulation in macroaggregates is that they harbor internal microaggregates (<0.25 mm) to offer more stable long-term storage for SOC (Zhang et al., 2014). According to Guo et al. (2020), soil aggregates with a diameter ranging from 1 to 2 mm exhibit a high degree of sensitivity to short-term disturbances. Macroaggregates are commonly employed as sensitivity indicators to assess the impact of land use change on organic carbon turnover because of their notable sensitivity and rapid turnover. The uncertainty surrounding the fate of SOC trapped by soil structure and aggregates across various land use types is of utmost importance in understanding anthropogenic climate change. The impacts of land management on structural stability and further SOC accumulation belowground are discussed in subsequent sections.

4.3. Symbiotic Relationship

Symbiosis is referred to as the close and long-term interaction between different biological species in which at least one associate of the pair benefits from the relationship. Nearly 80% of the land plants established a symbiotic relationship with fungi of the phylum Glomeromycota. Therefore, symbiotic interaction is a critical factor in SOC dynamics. The interactions between plants and microbes in the rhizosphere are crucial in determining plant growth and development and soil fertility. The symbiotic association between plant roots and (Arbuscular Mycorrhizae) AM fungi is ubiquitous in terrestrial ecosystems. The fungi penetrate the cells of plant roots and supply the plant with essential phosphates and other nutrients by extending its hyphae from the depletion zone of the soil. AM fungi primarily benefit from sugars produced by the plant through photosynthesis, which is the primary energy source for AMF. Several studies reported the importance of AMF interactions by concluding that higher amounts of SOM could be linked to fungal abundance and microbial biomass (Buckeridge et al., 2020; Kallenbach et al., 2016; Xu et al., 2018). Different pathways are involved in AMF, contributing to carbon fluxes between plants and the atmosphere (Fellbaum et al., 2012). One well-established mechanism via which AM) fungi capture carbon in soil involves the transfer of photosynthates from the host plants to the intraradical hyphae of the AM fungus and then to the extraradical hyphae before being released into the soil matrix (Parniske, 2008). However, the potential impact of AM fungi on soil carbon sequestration is contingent upon several factors, including the quantity of hyphal biomass generated, the duration of hyphal biomass turnover, and the involvement of these fungi in stabilizing soil aggregate formation. Fungal hyphae are composed of recalcitrant compounds that have a role in the deceleration of soil organic carbon cycle, and the lion's share of carbon transferred from plants to AMF is incorporated into extraradical hyphal biomass (Olsson & Johnson, 2005). Chitin is the primary cell wall component of the extraradical hyphae and is recalcitrant to decomposition. This symbiotic relationship can potentially improve belowground carbon accumulation by increasing net primary production, especially in conditions limited by nutrients. The stimulation of AM fungi by increased atmospheric CO_2 was assumed to be the primary mechanism that enhances soil carbon sequestration by augmenting the amount of carbon inputs to the soil and protecting organic carbon from degradation through aggregation. Numerous studies have demonstrated that a mycorrhizal connection substantially induces an extra carbon flux of 3-8% of gross photosynthesis into the soil (Gloor et al., 2012; Grimoldi et al., 2006). The rhizodeposition is another essential component of the terrestrial ecosystem that significantly influences plant-microbe interactions and subsequent carbon sequestration. Plant roots release a substantial amount of carbon absorbed during photosynthesis into the soil, often ranging from 5% to 30% (Philippot et al., 2010). Rhizodeposition can occur through several means, such as root exudates, mucilage, deceased root cells, and the transfer of rhizobacteria (Badri & Vivanco, 2009). The turnover of the mycorrhizal hyphae network is widely believed to be a primary and rapid mechanism for incorporating carbon into the soil organic matter pool, perhaps surpassing the inputs of shoot or root litter (Godbold et al., 2006). Plant species have different timescale ranges for transfer of photosynthetic carbon from plants to soil. Kuzyakov and Gavrichkova (2010), in their study of the time lag between photosynthesis and CO_2 efflux from the soil, concluded that the time scale can range from a few hours in grasses to a few days for trees. Most root exudate carbon is believed to be lost passively due to the significant difference in carbon content between the root cytoplasm and the apoplast/soil solution (Jones et al., 2009). Therefore, not all the carbon that is exuded into the soil comes from the roots; some of the carbon is allocated according to the size of the AM fungal hyphal network. Fungal hyphae produce the glycoprotein called glomalin that correlates with the hyphal length and stability of soil aggregates. Thus, glomalin protein, a significant factor in soil aggregate formation, is involved in carbon dynamics through physical protection and aggregate stabilization, as discussed in the previous section.

5. Impacts of Environmental Changes

The impacts of environmental changes on soil carbon dynamics, mediated by microbial activity, are multifaceted and interconnected. Climate change, particularly temperature and precipitation changes, directly influence soil microbial communities and their metabolic activities (Allison & Treseder, 2008). Shifts in microbial composition and activity affect organic matter decomposition rates and soil carbon sequestration (Rousk et al., 2009). Changes in temperature and moisture regimes can also impact the physical protection of soil organic carbon (SOC) within aggregates, influencing its stability and vulnerability to decomposition (Crowther et al., 2016).

Land use change, such as deforestation, urbanization, and agricultural expansion, dramatically alters soil microbial communities and their interactions with SOC (Foley et al., 2005). Conversion of natural ecosystems disrupts soil microbial habitats, leading to changes in microbial diversity, biomass, and activity (Bardgett et al., 2008). Consequently, organic matter decomposition and carbon sequestration rates may affect soil fertility, ecosystem functioning, and carbon storage capacity (Six et al., 2002).

Elevated atmospheric nitrogen deposition from human activities can impact soil microbial communities and functioning (Zhou et al., 2017). Changes in nitrogen cycling processes, including mineralization, nitrification, and denitrification, influence soil carbon dynamics (Liu et al., 2018). Shifts in nitrogen availability can affect the balance between carbon sequestration and greenhouse gas emissions in soils (Liu et al., 2018).

6. Strategies for Enhancing SOC through Microbial Activity and Land Use Management

Enhancing SOC through microbial activity involves fostering the conditions that promote the growth and sustain of soil microbes responsible for organic matter decomposition and carbon accumulation. Thus, land use practices and optimum microbial functioning are entangled, and management strategies determine the type, abundance, and activity of microbes in the soil (Fernández-Romero et al., 2014). However, the spatial distribution of SOC is majorly regulated by environmental and microclimatic conditions (Sattler et al., 2014). Two primary mechanisms of agricultural management improving carbon storage are increasing carbon inputs via high-yielding crops and decelerating the carbon released into the atmosphere (Smith & Read, 2010). Several agricultural management practices, such as fertilization, irrigation, mechanization, cover cropping, biochar application, crop diversification, and tilling practices, are general and widely followed, and a few of the strategies influencing SOC dynamics are discussed in the following sections.

6.1. Tillage Practices

It is a well-established fact that reduced or no-tillage mitigates SOC losses compared to more intensive plowing (Haddaway et al., 2017; Thotakuri et al., 2024; Varvel & Wilhelm, 2010). Soil tilling stimulates decomposition processes by direct physical disturbance due to plowing and indirectly through soil exposure to wet-dry and freeze-thaw cycles at the soil surface, dynamics in soil microclimate, and microbial community. However, mixed views are reported on the intensity of plowing influencing SOC storage. For example, Pan et al. (2010) reported an increase in the overall rate of 25.5 Tg carbon·yr^{-1} in SOC storage in the top 0 - 20 cm soil layer in their long-term study from 1985 to 2006. However, Blanco-Canqui et al. (2021), in their long-term study of tillage systems (39 yrs), concluded that no-till has limited potential in accumulating SOC near the soil surface but can enhance SOC stock for the soil profile compared to plow. Tillage has been done historically because of several benefits associated with the practice. These advantages include mechanically eliminating weeds, loosening, and aerating topsoil to facilitate planting and seedbed preparation, and mixing crop residues into the soil.

Conventional tillage, however, may lead to increased soil compaction below the plowing depth (i.e., creating a plow pan), increased vulnerability to wind and water erosion, and increased energy expenditures for the mechanical processes (Lal et al., 2007). No-till leaves the organic residues at the soil surface, reducing the surface runoff, increasing SOM, and promoting greater aggregate stability for mitigating erosion. The undisturbed residues serve as a readily available carbon source for the microbes residing on the surface layers of soil. The easily accessible food supply stimulates the growth and activity of microbial communities in the no-till system compared to conventional tilled soils. Microbes convert complex organic matter to simpler forms during decomposition.

Nonetheless, a fraction of the decomposed material undergoes humification, thus making it least susceptible to further decomposition and can endure for a more extended period. As discussed in the stability and mineralization section, microbes produce polysaccharides and other adhesive materials that bind soil particles together, forming stronger aggregates. These aggregates trap SOC and physically protect them from further decomposition by other microbes. Therefore, reduced secondary decomposition leads to a decrease in the CO_2 release back into the atmosphere, contributing to climate change mitigation. Although there are several advantages to no-till methods for sequestering SOC, it is important to consider other factors like soil type, climate, and location that can affect efficiency. Compared to tilled systems, long-term no-till systems may exhibit a decline in SOC deeper in the soil profile (Blanco-Canqui et al., 2021). Understanding these nuances is essential for improving no-till strategies at a regional scale, and it is a field of study being conducted.

6.2. Cover Diversification and Cover Crops

Crop diversification is adding more crops into existing crop rotation, or intercropping, annuals and perennials. Cover crops are defined as the crops ground to cover the ground, to protect the soil, from erosion and loss of nutrients to leaching and runoff, rather than for harvesting purposes. The two management strategies are promising in mitigating climate change and climate change and land degradation through soil and carbon sequestration while maintaining the ecosystem balance to ensure food security (Ebbisa, 2022; Francaviglia et al., 2017; Sanz et al., 2017). Monoculture farming, where a single crop is grown year after year, favors specific microbial populations adapted to utilizing the root exudates. This lack of diversity can limit organic matter decomposition and SOC sequestration efficiency. Crop diversification encourages microbial abundance and diversity in the population, promoting higher efficiency of SOM decomposition. Since crop diversification introduces a variety of plant species to the agricultural ecosystem, each plant species releases unique root exudates, fostering a more diverse microbial community. This diversity encourages microbes with a broader range of functionalities, allowing for the breakdown of complex organic matter from various sources. More specifically, increased plant-derived carbon inputs to soils in terms of quality, quantity, and chemical diversity lead to increased accumulation of SOC in agroecosystems with more diverse crop types.

This, in turn, promotes the development and diversity of soil microbial communities, improving SOC formation and storage (Zhang et al., 2021).

Additionally, different plant species have diverse root structures and depths. Crop rotations that include species with deep roots and those with shallow roots provide different soil layers access to a greater range of organic matter, encouraging more evenly distributed SOC storage across the profile. Cover crops, planted during fallow periods between main crop cycles, provide an additional and readily available carbon source for microbes. This stimulates their growth and activity, leading to increased decomposition of cover crop biomass and stable humic substances forming extended carbon storage. Cover crops cultivated in autumn and winter can also remove excess N from the soil and reduce N leaching. Cover crop roots provide pathways for air and water infiltration, while their decomposition products serve as soil particle binders, thus maintaining and improving soil structure by promoting aggregation. This enhanced structure supports microbial activity and protects SOC inside aggregates. However, climatic conditions (temperature and precipitation) impact the efficiency of cover crops in sequestering soil. For example, soils in cold temperate regions of the United States with high initial SOC levels tend to respond slower to cover crops than those in tropical environments (Blanco-Canqui, 2022). Implementing cover crops and crop diversification looks promising in promoting SOC sequestration, contributing to climate change mitigation, and improving water infiltration, fertility, and overall soil health, creating a more sustainable agriculture ecosystem.

6.3. Biochar Application

Biochar is a carbon-enriched and porous byproduct produced thermochemically by pyrolysis (heating in the absence of oxygen) of organic matter, which has emerged as a potential approach for enhancing SOC sequestration (Weng et al., 2017). The use of biochar in agriculture is still controversial because of its adverse priming effects, leading to a net carbon loss and emission potential of ~0.7 Pg C Eq·yr^{-1}. Although biochar is considered a reasonably stable component of SOC, soil biochar cannot be regarded as typically inert. Biochar application has a higher potential for SOC sequestration in the long term because of its high stability, but its decomposition pathways remain unclear (Schmidt et al., 2011). In addition, biochar has the ability to improve nutrient availability, soil water availability, microbial biomass, and soil microbial diversity, thus contributing to overall soil health and climate change mitigation (Glaser et al., 2015; Jeffery et al., 2017; Rogovska et al., 2014). The porous structure of biochar provides a harbor for existing SOC and physically shields SOC from further microbes, impeding their access to readily degradable organic matter. This protection is especially beneficial for labile carbon, encouraging its long-term storage. In addition, biochar's large surface area promotes adsorbing dissolved organic matter released by plant roots and microbial functioning, making the dissolved organic matter less susceptible to decomposition and contributing to SOC accumulation.

Soil aggregate development and stability can be aided by biochar. These aggregates, bound together by organic matter, including biochar and microbial byproducts, physically protect SOC from microbial decomposition. Liu et al. (2020), in their study of microbial carbon use, reported higher carbon sequestration potential with biochar amendment compared to straw. Biochar's decreased accessibility in organo-mineral interactions may contribute to soil stability. Chemical interactions with soil minerals and subsequent physical sealing in organo-mineral fractions can stabilize biochar, thus limiting its spatial availability to soil microbes (Fang et al., 2014). However, biochar mineralization can be increased by adding organic matter content to the soil. Though biochar is a recalcitrant carbon source, it may encumber N and P uptake by plants since biochar has a high affinity for these nutrients. Nutrient immobilization, eventually leading to limited plant growth and root exudation (critical carbon source for SOC formation), indirectly affects the SOC dynamics. In addition to interactions between biochar and soil, the stability of biochar-associated carbon in soil can be significantly impacted by soil environmental factors, such as temperature. Nguyen et al. (2010) reported a decline of biochar-associated carbon in their 1-year incubation study when temperature increased from 4˚C to 60˚C. Hence, it is crucial to consider the abiotic factors in biochar application to employ the full potential of biochar for mitigating climate change through enhanced carbon storage in the soil. Further investigation is still required to fully comprehend the long-term effects of biochar application on different soil types and microbial populations.

7. Future Work

A holistic understanding of the soil carbon pools and their interactions with biotic and abiotic factors helps arrive at more efficient strategies for managing soil health. Microbial carbon use efficiency (CUE) is the fraction of carbon uptake by microbes and retained as biomass and is an important factor in driving shifts in the diversity and structure of microbial communities. Previous works on the CUE followed multiple approaches, such as ^{13}C and ^{18}O labeling, calorespirometry, metabolic flux analysis, and stoichiometric modeling, reflecting methodological variability and limiting the ability to cross-compare published CUE values (Domeignoz-Horta et al., 2020; Sinsabaugh et al., 2016; Spohn et al., 2016). Therefore, accurately predicting soil carbon dynamics in different settings remains a major challenge. Further work on modeling accounting for abiotic factors such as temperature, moisture, oxygen limitation, and mineralogical interactions that have significant effects on the CUE can help reduce the methodological variability and arrive at congruence. However, interdisciplinary approaches must be applied to gain a broader understanding of soil carbon and microbe interactions. Advancements and collaborations with metagenomics help analyze and identify the key functional groups and metabolic pathways within the soil microbiome in carbon cycling. Inoculating soil with beneficial microbes like mycorrhizal fungi shows promise for better plant growth and potentially improving SOC sequestration. However, More research is needed on large-scale implementation and the ideal selection of effective microbial strains.

Additionally, developing integrated models with the holistic combination of soil physics, chemistry, and microbial biology aids in forecasting the long-term dynamics of soil carbon under various management strategies, thus helping to monitor the changes in SOC levels. The microbial carbon limitation is another key concept defining carbon cycling and ecosystem functioning with potential future research. The component pool sizes determine the amount of carbon in an ecosystem at any moment, and the carbon fluxes into and out of terrestrial ecosystems are regulated by the rates of processes like photosynthesis, respiration, and growth, which may be sensitive to environmental change. These processes are limited by the pace of the slowest factor, carbon uptake. Understanding how the carbon limitation of soil decomposers drives the ecological processes might help resolve the diverse belowground reactions to non-steady state conditions. The advent of new molecular techniques allows better monitoring of growth responses of microbial communities, even individual taxa, which allows decomposer's limitations to be better tested and quantified.

8. Summary

This overview highlighted the complex relationship between soil carbon and microbes. The activity of microorganisms substantially influences soil organic carbon through processes such as aggregation, decomposition, and symbiotic interactions. Gaining a comprehensive understanding of these interactions is essential for developing successful techniques to improve the sequestration of SOC. Land-use management strategies such as reduced tillage, cover cropping, and biochar application have been proven to enhance advantageous microbial populations and eventually increase the storage of SOC. Channeling the power of soil microbes through optimal land-use practices and fostering their resilience helps mitigate the climatic changes and their subsequent effect on soil health to an extent. Given the potential threat to soil health from many abiotic factors, it is imperative to do further study to comprehend microbial adaptability and develop methods to promote robust microbial populations in response to a changing climate.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

References

Allison, S. D., & Treseder, K. K. (2008). Warming and Drying Suppress Microbial Activity and Carbon Cycling in Boreal Forest Soils. *Global Change Biology, 14,* 2898-2909. https://doi.org/10.1111/j.1365-2486.2008.01716.x

Badri, D. V., & Vivanco, J. M. (2009). Regulation and Function of Root Exudates. *Plant,* *Cell & Environment, 32*, 666-681. https://doi.org/10.1111/j.1365-3040.2009.01926.x

Bardgett, R. D., Freeman, C., & Ostle, N. J. (2008). Microbial Contributions to Climate Change through Carbon Cycle Feedbacks. *The ISME Journal, 2,* 805-814. https://doi.org/10.1038/ismej.2008.58

Bastida, F., Eldridge, D. J., García, C., Kenny Png, G., Bardgett, R. D., & Delgado-Baquerizo, M. (2021). Soil Microbial Diversity-Biomass Relationships Are Driven by Soil Carbon Content across Global Biomes. *The ISME Journal, 15,* 2081-2091. https://doi.org/10.1038/s41396-021-00906-0

Berendsen, R. L., Pieterse, C. M., & Bakker, P. A. (2012). The Rhizosphere Microbiome and Plant Health. *Trends in Plant Science, 17,* 478-486. https://doi.org/10.1016/j.tplants.2012.04.001

Blanco-Canqui, H. (2022). Cover Crops and Carbon Sequestration: Lessons from US Studies. *Soil Science Society of America Journal, 86,* 501-519. https://doi.org/10.1002/saj2.20378

Blanco-Canqui, H., & Lal, R. (2004). Mechanisms of Carbon Sequestration in Soil Aggregates. *Critical Reviews in Plant Sciences, 23*, 481-504. https://doi.org/10.1080/07352680490886842

Blanco-Canqui, H., Shapiro, C., Jasa, P., & Iqbal, J. (2021). No-Till and Carbon Stocks: Is Deep Soil Sampling Necessary? Insights from Long-Term Experiments. *Soil and Tillage Research, 206,* Article ID: 104840. https://doi.org/10.1016/j.still.2020.104840

Buckeridge, K. M., La Rosa, A. F., Mason, K. E., Whitaker, J., McNamara, N. P., Grant, H. K., & Ostle, N. J. (2020). Sticky Dead Microbes: Rapid Abiotic Retention of Microbial Necromass in Soil. *Soil Biology and Biochemistry, 149*, Article ID: 107929. https://doi.org/10.1016/j.soilbio.2020.107929

Cleveland, C. C., & Liptzin, D. (2007). C:N:P Stoichiometry in Soil: Is There a "Redfield Ratio" for the Microbial Biomass? *Biogeochemistry, 85,* 235-252. https://doi.org/10.1007/s10533-007-9132-0

Craine, J., Wedin, D., Chapin, F., & Reich, P. (2003). Relationship between the Structure of Root Systems and Resource Use for 11 North American Grassland Plants. *Plant Ecology, 165,* 85-100. https://doi.org/10.1023/A:1021414615001

Crowther, T. W., Todd-Brown, K. E., Rowe, C. W., Wieder, W. R., Carey, J. C., Machmuller, M. B., Snoek, B., Fang, S., Zhou, G., & Allison, S. D. (2016). Quantifying Global Soil Carbon Losses in Response to Warming. *Nature, 540,* 104-108. https://doi.org/10.1038/nature20150

DeAngelis, K. M., Brodie, E. L., DeSantis, T. Z., Andersen, G. L., Lindow, S. E., & Firestone, M. K. (2009). Selective Progressive Response of Soil Microbial Community to Wild Oat Roots. *The ISME Journal, 3,* 168-178. https://doi.org/10.1038/ismej.2008.103

Delgado-Baquerizo, M., Oliverio, A. M., Brewer, T. E., Benavent-González, A., Eldridge, D. J., Bardgett, R. D., Maestre, F. T., Singh, B. K., & Fierer, N. (2018). A Global Atlas of the Dominant Bacteria Found in Soil. *Science, 359,* 320-325. https://doi.org/10.1126/science.aap9516

Domeignoz-Horta, L. A., Pold, G., Liu, X.-J. A., Frey, S. D., Melillo, J. M., & DeAngelis, K. M. (2020). Microbial Diversity Drives Carbon Use Efficiency in a Model Soil. *Nature Communications, 11,* Article No. 3684. https://doi.org/10.1038/s41467-020-17502-z

Ebbisa, A. (2022). Mechanisms Underlying Cereal/Legume Intercropping as Nature-Based Biofortification: A Review. *Food Production, Processing and Nutrition, 4,* 19. https://doi.org/10.1186/s43014-022-00096-y

Falkowski, P. G., Fenchel, T., & Delong, E. F. (2008). The Microbial Engines That Drive

Earth's Biogeochemical Cycles. *Science, 320,* 1034-1039.
https://doi.org/10.1126/science.1153213

Fang, H., Cheng, S., Yu, G., Xu, M., Wang, Y., Li, L., Dang, X., Wang, L., & Li, Y. (2014). Experimental Nitrogen Deposition Alters the Quantity and Quality of Soil Dissolved Organic Carbon in an Alpine Meadow on the Qinghai-Tibetan Plateau. *Applied Soil Ecology, 81,* 1-11. https://doi.org/10.1016/j.apsoil.2014.04.007

Fellbaum, C. R., Gachomo, E. W., Beesetty, Y., Choudhari, S., Strahan, G. D., Pfeffer, P. E., Kiers, E. T., & Bücking, H. (2012). Carbon Availability Triggers Fungal Nitrogen Uptake and Transport in Arbuscular Mycorrhizal Symbiosis. *Proceedings of the National Academy of Sciences*, *109*, 2666-2671. https://doi.org/10.1073/pnas.1118650109

Fernández-Romero, M., Lozano-García, B., & Parras-Alcántara, L. (2014). Topography and Land Use Change Effects on the Soil Organic Carbon Stock of Forest Soils in Mediterranean Natural Areas. *Agriculture, Ecosystems & Environment, 195,* 1-9.
https://doi.org/10.1016/j.agee.2014.05.015

Fierer, N., & Jackson, R. B. (2006). The Diversity and Biogeography of Soil Bacterial Communities. *Proceedings of the National Academy of Sciences, 103,* 626-631.
https://doi.org/10.1073/pnas.0507535103

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., & Gibbs, H. K. (2005). Global Consequences of Land Use. *Science, 309,* 570-574. https://doi.org/10.1126/science.1111772

Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., & Rumpel, C. (2007). Stability of Organic Carbon in Deep Soil Layers Controlled by Fresh Carbon Supply. *Nature, 450,* 277-280. https://doi.org/10.1038/nature06275

Francaviglia, R., Di Bene, C., Farina, R., & Salvati, L. (2017). Soil Organic Carbon Sequestration and Tillage Systems in the Mediterranean Basin: A Data Mining Approach. *Nutrient Cycling in Agroecosystems, 107,* 125-137.
https://doi.org/10.1007/s10705-016-9820-z

Giller, K. E., Witter, E., & Mcgrath, S. P. (1998). Toxicity of Heavy Metals to Microorganisms and Microbial Processes in Agricultural Soils: A Review. *Soil Biology and Biochemistry, 30,* 1389-1414. https://doi.org/10.1016/S0038-0717(97)00270-8

Glaser, B., Wiedner, K., Seelig, S., Schmidt, H.-P., & Gerber, H. (2015). Biochar Organic Fertilizers from Natural Resources as Substitute for Mineral Fertilizers. *Agronomy for Sustainable Development, 35,* 667-678. https://doi.org/10.1007/s13593-014-0251-4

Gloor, M., Gatti, L., Brienen, R., Feldpausch, T., Phillips, O., Miller, J., Ometto, J., Rocha, H., Baker, T., & De Jong, B. (2012). The Carbon Balance of South America: A Review of the Status, Decadal Trends and Main Determinants. *Biogeosciences*, *9*, 5407-5430.
https://doi.org/10.5194/bg-9-5407-2012

Godbold, D. L., Hoosbeek, M. R., Lukac, M., Cotrufo, M. F., Janssens, I. A., Ceulemans, R., Polle, A., Velthorst, E. J., Scarascia-Mugnozza, G., & De Angelis, P. (2006). Mycorrhizal Hyphal Turnover as a Dominant Process for Carbon Input into Soil Organic Matter. *Plant and Soil*, *281*, 15-24. https://doi.org/10.1007/s11104-005-3701-6

Gougoulias, C., Clark, J. M., & Shaw, L. J. (2014). The Role of Soil Microbes in the Global Carbon Cycle: Tracking the Below-Ground Microbial Processing of Plant-Derived Carbon for Manipulating Carbon Dynamics in Agricultural Systems. *Journal of the Science of Food and Agriculture, 94,* 2362-2371. https://doi.org/10.1002/jsfa.6577

Grimoldi, A. A., Kavanová, M., Lattanzi, F. A., Schäufele, R., & Schnyder, H. (2006). Arbuscular Mycorrhizal Colonization on Carbon Economy in Perennial Ryegrass: Quantification by $^{13}CO_2/^{12}CO_2$ Steady-State Labelling and Gas Exchange. *New Phytologist*, *172*, 544-553. https://doi.org/10.1111/j.1469-8137.2006.01853.x

Guo, Y., Fan, R., Zhang, X., Zhang, Y., Wu, D., McLaughlin, N., Zhang, S., Chen, X., Jia, S., & Liang, A. (2020). Tillage-Induced Effects on SOC through Changes in Aggregate Stability and Soil Pore Structure. *Science of the Total Environment*, *703*, Article ID: 134617. https://doi.org/10.1016/j.scitotenv.2019.134617

Haddaway, N. R., Hedlund, K., Jackson, L. E., Kätterer, T., Lugato, E., Thomsen, I. K., Jørgensen, H. B., & Isberg, P.-E. (2017). How Does Tillage Intensity Affect Soil Organic Carbon? A Systematic Review. *Environmental Evidence, 6,* 1-48. https://doi.org/10.1186/s13750-016-0079-2

Hossain, M. B., Rahman, M. M., Biswas, J. C., Miah, M. M. U., Akhter, S., Maniruzzaman, M., Choudhury, A. K., Ahmed, F., Shiragi, M. H. K., & Kalra, N. (2017). Carbon Mineralization and Carbon Dioxide Emission from Organic Matter Added Soil under Different Temperature Regimes. *International Journal of Recycling of Organic Waste in Agriculture*, *6*, 311-319. https://doi.org/10.1007/s40093-017-0179-1

Jeffery, S., Abalos, D., Prodana, M., Bastos, A. C., Van Groenigen, J. W., Hungate, B. A., & Verheijen, F. (2017). Biochar Boosts Tropical but Not Temperate Crop Yields. *Environmental Research Letters, 12,* Article ID: 053001. https://doi.org/10.1088/1748-9326/aa67bd

Jones, D. L., Nguyen, C., & Finlay, R. D. (2009). *Carbon Flow in the Rhizosphere: Carbon Trading at the Soil-Root Interface*. Springer. https://doi.org/10.1007/s11104-009-9925-0

Kallenbach, C. M., Frey, S. D., & Grandy, A. S. (2016). Direct Evidence for Microbial-Derived Soil Organic Matter Formation and Its Ecophysiological Controls. *Nature Communications*, *7*, Article No. 13630. https://doi.org/10.1038/ncomms13630

Khatoon, H., Solanki, P., Narayan, M., Tewari, L., Rai, J., & Hina Khatoon, C. (2017). Role of Microbes in Organic Carbon Decomposition and Maintenance of Soil Ecosystem. *International Journal of Chemical Studies*, *5*, 1648-1656.

Kögel-Knabner, I., Ekschmitt, K., Flessa, H., Guggenberger, G., Matzner, E., Marschner, B., & von Lützow, M. (2008). *An Integrative Approach of Organic Matter Stabilization in Temperate Soils: Linking Chemistry, Physics, and Biology. Journal of Plant Nutrition and Soil Science*, *171*, 5-13. https://doi.org/10.1002/jpln.200700215

Kuzyakov, Y., & Gavrichkova, O. (2010). Time Lag between Photosynthesis and Carbon Dioxide Efflux from Soil: A Review of Mechanisms and Controls. *Global Change Biology*, *16*, 3386-3406. https://doi.org/10.1111/j.1365-2486.2010.02179.x

Lal, R. (2016). Soil Health and Carbon Management. *Food and Energy Security*, *5*, 212-222. https://doi.org/10.1002/fes3.96

Lal, R., Follett, R. F., Stewart, B. A., & Kimble, J. M. (2007). Soil Carbon Sequestration to Mitigate Climate Change and Advance Food Security. *Soil Science*, *172*, 943-956. https://doi.org/10.1097/ss.0b013e31815cc498

Lauber, C. L., Strickland, M. S., Bradford, M. A., & Fierer, N. (2008). The Influence of Soil Properties on the Structure of Bacterial and Fungal Communities across Land-Use Types. *Soil Biology and Biochemistry, 40,* 2407-2415. https://doi.org/10.1016/j.soilbio.2008.05.021

Liu, X., Yang, T., Wang, Q., Huang, F., & Li, L. (2018). Dynamics of Soil Carbon and Nitrogen Stocks after Afforestation in Arid and Semi-Arid Regions: A Meta-Analysis. *Science of the Total Environment, 618,* 1658-1664. https://doi.org/10.1016/j.scitotenv.2017.10.009

Liu, Z., Wu, X., Liu, W., Bian, R., Ge, T., Zhang, W., Zheng, J., Drosos, M., Liu, X., & Zhang, X. (2020). Greater Microbial Carbon Use Efficiency and Carbon Sequestration in Soils: Amendment of Biochar versus Crop Straws. *GCB Bioenergy, 12,* 1092-1103. https://doi.org/10.1111/gcbb.12763

McCulley, R. L., Burke, I. C., Nelson, J. A., Lauenroth, W. K., Knapp, A. K., & Kelly, E. F. (2005). Regional Patterns in Carbon Cycling across the Great Plains of North America. *Ecosystems, 8,* 106-121. https://doi.org/10.1007/s10021-004-0117-8

Nguyen, B. T., Lehmann, J., Hockaday, W. C., Joseph, S., & Masiello, C. A. (2010). Temperature Sensitivity of Black Carbon Decomposition and Oxidation. *Environmental Science & Technology, 44,* 3324-3331. https://doi.org/10.1021/es903016y

Olsson, P. A., & Johnson, N. C. (2005). Tracking Carbon from the Atmosphere to the Rhizosphere. *Ecology Letters*, *8*, 1264-1270. https://doi.org/10.1111/j.1461-0248.2005.00831.x

Omar, Z., Bouajila, A., Chniguir, N., & Hamed, Y. (2023). Organic Matter Mineralization, Aggregation, and Aggregate-Associated Organic Carbon in Saline Soil of Arid Region of Tunisia: A Laboratory Incubation. *Arabian Journal of Geosciences*, *16*, Article No. 554. https://doi.org/10.1007/s12517-023-11676-8

Pan, G., Xu, X., Smith, P., Pan, W., & Lal, R. (2010). An Increase in Topsoil SOC Stock of China's Croplands between 1985 and 2006 Revealed by Soil Monitoring. *Agriculture, Ecosystems & Environment, 136,* 133-138. https://doi.org/10.1016/j.agee.2009.12.011

Parniske, M. (2008). Arbuscular Mycorrhiza: The Mother of Plant Root Endosymbioses. *Nature Reviews Microbiology*, *6*, 763-775. https://doi.org/10.1038/nrmicro1987

Philippot, L., Andersson, S. G., Battin, T. J., Prosser, J. I., Schimel, J. P., Whitman, W. B., & Hallin, S. (2010). The Ecological Coherence of High Bacterial Taxonomic Ranks. *Nature Reviews Microbiology, 8,* 523-529. https://doi.org/10.1038/nrmicro2367

Poll, C., Marhan, S., Ingwersen, J., & Kandeler, E. (2008). Dynamics of Litter Carbon Turnover and Microbial Abundance in a Rye Detritusphere. *Soil Biology and Biochemistry, 40,* 1306-1321. https://doi.org/10.1016/j.soilbio.2007.04.002

Ramesh, T., Bolan, N. S., Kirkham, M. B., Wijesekara, H., Kanchikerimath, M., Rao, C. S., Sandeep, S., Rinklebe, J., Ok, Y. S., & Choudhury, B. U. (2019). Soil Organic Carbon Dynamics: Impact of Land Use Changes and Management Practices: A Review. *Advances in Agronomy*, *156*, 1-107. https://doi.org/10.1016/bs.agron.2019.02.001

Rogovska, N., Laird, D. A., Rathke, S. J., & Karlen, D. L. (2014). Biochar Impact on Midwestern Mollisols and Maize Nutrient Availability. *Geoderma, 230,* 340-347. https://doi.org/10.1016/j.geoderma.2014.04.009

Rousk, J., Brookes, P. C., & Bååth, E. (2009). Contrasting Soil pH Effects on Fungal and Bacterial Growth Suggest Functional Redundancy in Carbon Mineralization. *Applied and Environmental Microbiology, 75,* 1589-1596. https://doi.org/10.1128/AEM.02775-08

Sanz, M., De Vente, J., Chotte, J.-L., Bernoux, M., Kust, G., Ruiz, I., Almagro, M., Alloza, J., Vallejo, R., & Castillo, V. (2017). *Sustainable Land Management Contribution to Successful Land-Based Climate Change Adaptation and Mitigation: A Report of the Science-Policy Interface*. United Nations Convention to Combat Desertification (UNCCD).

Sattler, D., Murray, L. T., Kirchner, A., & Lindner, A. (2014). Influence of Soil and Topography on Aboveground Biomass Accumulation and Carbon Stocks of Afforested Pastures in South East Brazil. *Ecological Engineering, 73,* 126-131. https://doi.org/10.1016/j.ecoleng.2014.09.003

Schimel, J. P., & Schaeffer, S. M. (2012). Microbial Control over Carbon Cycling in Soil. *Frontiers in Microbiology, 3,* Article No. 348. https://doi.org/10.3389/fmicb.2012.00348

Schjønning, P., Elmholt, S., & Christensen, B. T. (2004). *Managing Soil Quality: Challenges in Modern Agriculture*. CABI. https://doi.org/10.1079/9780851996714.0000

Schmidt, M. W., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., & Manning, D. A. (2011). Persistence of

Soil Organic Matter as an Ecosystem Property. *Nature, 478,* 49-56. https://doi.org/10.1038/nature10386

Serrano, O., Ricart, A. M., Lavery, P. S., Mateo, M. A., Arias-Ortiz, A., Masque, P., Rozaimi, M., Steven, A., & Duarte, C. M. (2016). Key Biogeochemical Factors Affecting Soil Carbon Storage in Posidonia Meadows. *Biogeosciences, 13,* 4581-4594. https://doi.org/10.5194/bg-13-4581-2016

Singh, B. K., Bardgett, R. D., Smith, P., & Reay, D. S. (2010). Microorganisms and Climate Change: Terrestrial Feedbacks and Mitigation Options. *Nature Reviews Microbiology, 8,* 779-790. https://doi.org/10.1038/nrmicro2439

Sinsabaugh, R. L., Turner, B. L., Talbot, J. M., Waring, B. G., Powers, J. S., Kuske, C. R., Moorhead, D. L., & Shah, J. J. F. (2016). Stoichiometry of Microbial Carbon Use Efficiency in Soils. *Ecological Monographs, 86,* 172-189. https://doi.org/10.1890/15-2110.1

Six, J., Conant, R. T., Paul, E. A., & Paustian, K. (2002). Stabilization Mechanisms of Soil Organic Matter: Implications for C-Saturation of Soils. *Plant and Soil, 241,* 155-176. https://doi.org/10.1023/A:1016125726789

Six, J., Elliott, E. T., & Paustian, K. (2000). Soil Macroaggregate Turnover and Microaggregate Formation: A Mechanism for C Sequestration under No-Tillage Agriculture. *Soil Biology and Biochemistry, 32,* 2099-2103. https://doi.org/10.1016/S0038-0717(00)00179-6

Smith, S. E., & Read, D. J. (2010). *Mycorrhizal Symbiosis*. Academic Press.

Sokol, N. W., Slessarev, E., Marschmann, G. L., Nicolas, A., Blazewicz, S. J., Brodie, E. L., Firestone, M. K., Foley, M. M., Hestrin, R., & Hungate, B. A. (2022). Life and Death in the Soil Microbiome: How Ecological Processes Influence Biogeochemistry. *Nature Reviews Microbiology, 20,* 415-430. https://doi.org/10.1038/s41579-022-00695-z

Spaccini, R., Piccolo, A., Conte, P., Haberhauer, G., & Gerzabek, M. (2002). Increased Soil Organic Carbon Sequestration through Hydrophobic Protection by Humic Substances. *Soil Biology and Biochemistry, 34,* 1839-1851. https://doi.org/10.1016/S0038-0717(02)00197-9

Spohn, M., Klaus, K., Wanek, W., & Richter, A. (2016). Microbial Carbon Use Efficiency and Biomass Turnover Times Depending on Soil Depth-Implications for Carbon Cycling. *Soil Biology and Biochemistry, 96,* 74-81. https://doi.org/10.1016/j.soilbio.2016.01.016

Thotakuri, G., Chakraborty, P., Singh, J., Xu, S., Kovács, P., Iqbal, J., & Kumar, S. (2024). X-Ray Computed Tomography—Measured Pore Characteristics and Hydro-Physical Properties of Soil Profile as Influenced by Long-Term Tillage and Rotation Systems. *Catena, 237,* Article ID: 107801. https://doi.org/10.1016/j.catena.2023.107801

Van Der Heijden, M. G., Bardgett, R. D., & Van Straalen, N. M. (2008). The Unseen Majority: Soil Microbes as Drivers of Plant Diversity and Productivity in Terrestrial Ecosystems. *Ecology Letters, 11,* 296-310. https://doi.org/10.1111/j.1461-0248.2007.01139.x

Vandenkoornhuyse, P., Quaiser, A., Duhamel, M., Le Van, A., & Dufresne, A. (2015). The Importance of the Microbiome of the Plant Holobiont. *New Phytologist, 206,* 1196-1206. https://doi.org/10.1111/nph.13312

Varvel, G., & Wilhelm, W. (2010). Long-Term Soil Organic Carbon as Affected by Tillage and Cropping Systems. *Soil Science Society of America Journal, 74,* 915-921. https://doi.org/10.2136/sssaj2009.0362

Wallenstein, M. D., & Burns, R. G. (2011). Ecology of Extracellular Enzyme Activities and Organic Matter Degradation in Soil: A Complex Community-Driven Process. *Methods of Soil Enzymology, 9,* 35-55. https://doi.org/10.2136/sssabookser9.c2

Weng, Z., Van Zwieten, L., Singh, B. P., Tavakkoli, E., Joseph, S., Macdonald, L. M., Rose,

T. J., Rose, M. T., Kimber, S. W., & Morris, S. (2017). Biochar Built Soil Carbon over a Decade by Stabilizing Rhizodeposits. *Nature Climate Change, 7,* 371-376. https://doi.org/10.1038/nclimate3276

Wieder, W. R., Bonan, G. B., & Allison, S. D. (2013). Global Soil Carbon Projections Are Improved by Modelling Microbial Processes. *Nature Climate Change, 3,* 909-912. https://doi.org/10.1038/nclimate1951

Wu, M., Chen, L., Ma, J., Zhang, Y., Li, X., & Pang, D. (2023). Aggregate-Associated Carbon Contributes to Soil Organic Carbon Accumulation along the Elevation Gradient of Helan Mountains. *Soil Biology and Biochemistry, 178,* Article ID: 108926. https://doi.org/10.1016/j.soilbio.2022.108926

Xu, J., Liu, S., Song, S., Guo, H., Tang, J., Yong, J. W., Ma, Y., & Chen, X. (2018). Arbuscular Mycorrhizal Fungi Influence Decomposition and the Associated Soil Microbial Community under Different Soil Phosphorus Availability. *Soil Biology and Biochemistry*, *120*, 181-190. https://doi.org/10.1016/j.soilbio.2018.02.010

Yu, H., Ding, W., Chen, Z., Zhang, H., Luo, J., & Bolan, N. (2015). Accumulation of Organic C components in Soil and Aggregates. *Scientific Reports*, *5*, Article No. 13804. https://doi.org/10.1038/srep13804

Zhang, B., Chen, S., He, X., Liu, W., Zhao, Q., Zhao, L., & Tian, C. (2014). Responses of Soil Microbial Communities to Experimental Warming in Alpine Grasslands on the Qinghai-Tibet Plateau. *PLOS ONE, 9,* e103859. https://doi.org/10.1371/journal.pone.0103859

Zhang, K., Maltais-Landry, G., & Liao, H.-L. (2021). How Soil Biota Regulate C Cycling and Soil C Pools in Diversified Crop Rotations. *Soil Biology and Biochemistry, 156,* Article ID: 108219. https://doi.org/10.1016/j.soilbio.2021.108219

Zhou, Z., Wang, C., Zheng, M., Jiang, L., & Luo, Y. (2017). Patterns and Mechanisms of Responses by Soil Microbial Communities to Nitrogen Addition. *Soil Biology and Biochemistry*, *115*, 433-441. https://doi.org/10.1016/j.soilbio.2017.09.015