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Microbial contribution to the carbon flux in the soil: A literature review

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ABSTRACT: Carbon flows into and out of the soil are important processes that contribute to controlling the global climate. The relationship between soil organisms and the climate is interdependent since the organisms that contribute to carbon and greenhouse gas fluxes are simultaneously affected by climate change and soil management. Temperature, soil moisture, pH, nutrient level, redox potential and organic matter quality are key elements affecting the microorganisms involved in organic carbon flows in the soil. Climate, topography (slope and position in the landscape), soil texture, soil mineralogy and land-use regulate those key elements and, thus, the C fluxes in the pedosphere. Soil microbes can increase carbon influx and storage by promoting plant growth, mycorrhizal establishment, and particle aggregation. Conversely, microorganisms contribute to carbon efflux from the soil via methanogenesis, rhizospheric activity, and organic carbon mineralization. Nevertheless, strategies and management practices could be used to balance out carbon emissions to the atmosphere. For example, carbon influx and storage in the soil can be stimulated by plant growth promoting microorganisms, greater plant diversity via crop rotation and cover crops, cultivating mycotrophic plants, avoiding or reducing the use of fungicides and adopting organic farming, no-tillage crop systems and conservative soil management strategies. Therefore, this review aimed to shed light on how soil microorganisms can contribute to increase C influxes to the soil, and its significance for climate change. Then, we also seek to gather the practical actions proposed in the scientific literature to improve carbon sequestration and storage in the soil. In summary, the review provides a comprehensive basis on soil microorganisms as key to carbon fluxes and helpers to lessen climate change by increasing carbon fixation and storage in agroecosystems via stimulation or application of beneficial microorganisms.

Keywords: carbon cycle, soil microorganisms, climate change, soil organic carbon, carbon sequestration.

INTRODUCTION

Soil organic carbon (SOC) plays essential roles in terrestrial ecosystem function by providing a basis for primary production, including agrarian yields (Wiesmeier et al., 2019), improving water holding capacity (Werner et al., 2020), and regulating the climate (Lal et al., 2021). These benefits result from the impact organic matter has on soil aggregation (Tisdall and Oades, 1982), nutrient availability (Murphy, 2014), water storage and filtering (Werner et al., 2020), and C storage (Lal et al., 2021).

Soil carbon exists in three forms: inorganic C, elementary C, or organic C as organic matter (Batjes, 2014). Inorganic carbon occurs as carbonates from the soil's parent material or as precipitated anions from previously solubilized atmospheric CO_2 (Zamanian et al., 2016). Carbonate levels are only significant in soils formed from parent material rich in carbonates and where relief and water regimes prevent removal, as in drier (arid and semi-arid) regions where precipitation is insufficient to solubilize and leach carbonates (Zamanian et al., 2016). However, most soil carbon (C) is found in organic molecules from plant matter. Subsequent chemical diversification results from catabolic and anabolic activity in the soil.

Fluxes in and out of the soil determine organic carbon stock. Organic material originates from deposited leaves, branches, flowers and roots (Villarino et al., 2021). Organic substances function as both a source of energy for both plants and all other chemoorganotrophic organisms and a stock of carbon (Batjes, 2014; Lal et al., 2021). The substrates can be used as energy sources for cellular processes, including respiration, that result in the oxidation of carbon and emission of CO_2 back into the atmosphere (Haaf et al., 2021). Concurrently, the variety of organic molecules derived from plants increases in the soil. Both chemoorganotrophic and chemolithotrophic organisms synthesize new organic molecules through anabolism for cell maintenance and proliferation and catabolism-based byproduct formation (Li et al., 2018).

Decomposition and mineralization of organic material on the soil result in soluble C molecules, CO_2, and humic substances. Wetter conditions allow soluble molecules containing C to migrate vertically in the soil and leach into bodies of ground and surface water (Gmach et al., 2020; Nakhavali et al., 2021). In this process, some organic molecules can complex with Al, move downwards, and accumulate in subsurface horizons, such as in the Podzols. The loss of organic carbon through water movement is significant under specific circumstances, such as sandy forest soils and soils with coarse textures that receive substantial amounts of organic material and precipitation (Yost and Hartemink, 2019). In fact, most SOC stock is regulated by the influx of organic matter deposition and efflux by soil mineralization performed by soil microorganisms (Zhang et al., 2020; Tang et al., 2022). Thus, soil microorganisms play important roles in soil ecological processes due to their impact on C fluxes.

Greenhouse gas emissions, mainly as CO_2 and CH_4 efflux, have been increasing due to human activities (Masson-Delmotte et al., 2021). The consequences of the emissions lie in ecological functioning disruptions and extreme events, which affect social and economic activities. On the other hand, mitigation practices for climate change have been proposed; for example, to improve C sequestration and storage in the soil. Some microorganisms contribute both to carbon sequestration through photosynthesis stimulation and carbon storage through hyphae growth and/or particle aggregation that protect the organic matter against biodegradation (Morris et al., 2019; Adeleke and Babalola, 2021; Hakim et al., 2021). Thus, there is the potential to apply or manage soil microorganisms to offset carbon emissions.

However, gathering basic and applied knowledge about the functions of soil microbiota for carbon flux is necessary to better understand the processes involved and support microbial management to counterbalance soil emissions in a changing climate scenario.

Given the roles of organic carbon in the soil for functions of terrestrial ecosystems and for climate regulation, this review aims to provide a comprehensive basis on soil microorganisms as keys to carbon fluxes and to present the perspectives of using beneficial microorganisms as helpers to lessen climate change by increasing carbon fixation and storage in agroecosystems.

MICROORGANISMS AND CARBON FLUXES THROUGH THE SOIL

Soil is as a significant carbon reservoir, containing three times more carbon than vegetation and two times more than the atmosphere (Figure 1). Nevertheless, C reservoirs in the soil are continually under threat from deforestation of tropical forests, agricultural management practices such as tilling, and environmental change such as permafrost thawing. Some estimates show that the top 1 m of soil across the planet may contain from 2157 to 2293 Pg of C, of which 1462 to 1548 Pg is organic C and 695 to 748 Pg is inorganic C (Figure 1) (Batjes, 2014). Estimates of C fixed by photosynthesis in land ecosystems vary considerably from 120 to 178 Pg C yr^{-1} (gross primary production - GPP) (Canadell et al., 2021; Jian et al., 2022), with 60 Pg C yr^{-1} entering the soil (Figure 1) (Canadell et al., 2021). Part of this C is used by plant metabolism, while organic C entering the soil is used by chemoorganotrophics. Approximately 115 Pg yr^{-1} of C-CO$_2$ is emitted to the atmosphere through aerobic respiration by soil organisms (55 Pg yr^{-1}) and plant communities (60 yr^{-1}) (Canadell et al., 2021). Soil methanogenic contributions to CH$_4$ emissions are poorly understood but may reach 0.5 Pg yr^{-1} (Feng et al., 2022). Methane-oxidizing microorganisms also contribute to CO$_2$ emissions (Tang et al., 2022).

Considering the multi-function mechanisms for structuring and organizing the soils and its associate microbiota, studies on soil habitat are fundamental to better understand the C fluxes during environmental change. Microorganism diversity, abundance and activity vary greatly among soils. The number of species within a gram of soil can range from 10^3 to 10^6 (Torsvik et al., 1996; Dykhuizen, 2005; Roesch et al., 2007). These highly diverse communities play an essential role in terrestrial ecosystems by contributing to several ecological processes, such as the mineralization of organic matter, nutrient cycling (Coonan et al., 2020; Yadav et al., 2021), and mineral solubilization (Billah et al., 2019; Rawat et al., 2021). Soil microorganisms also affect physical properties of
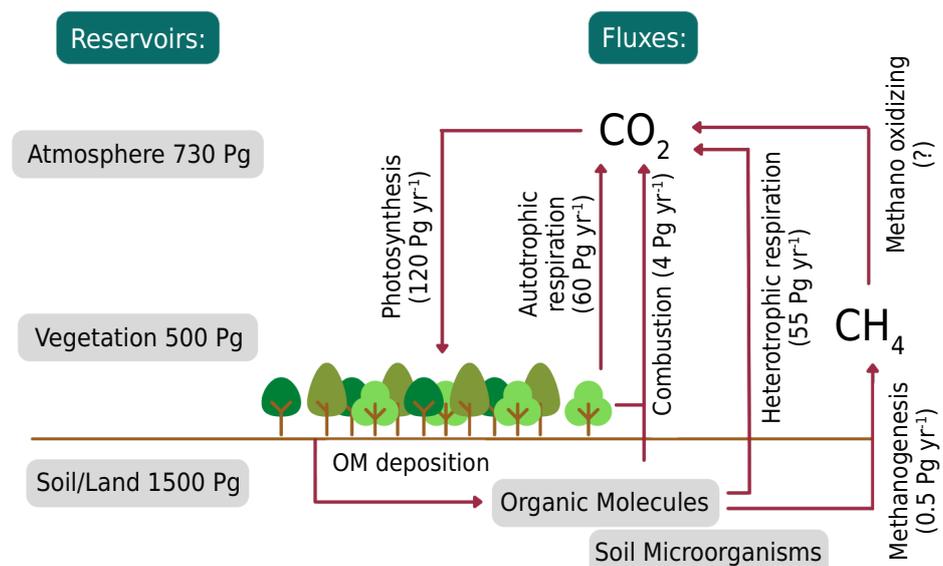

Figure 1. CO$_2$ fixation, organic molecules entering the soil, metabolization by soil microorganisms, and emissions of CO$_2$ and CH$_4$ to the atmosphere. Numbers are Pg flows per year (arrows) and average quantities in reservoirs (Canadell et al., 2021; Feng et al., 2022).

the soil by actively contributing to soil habitat formation, actuating C deposition, and forming aggregates (Costa et al., 2018; Morris et al., 2019). Soil microorganisms establish mutualistic associations with plants (Afkhami et al., 2020) and animals (Arora et al., 2021) and consequently regulate the abundance of living organisms (Sokol et al., 2022a). In parallel, the great biodiversity of these microorganisms represents a diverse set of metabolic routes or genes/enzymes that can be used in agrarian, medical, industrial, urban and environmental areas (Vanacek et al., 2018; Dey, 2022; Sousa et al., 2022).

Soil microbial communities contribute to global climate regulation by emitting greenhouse gases (GHG), mainly CO_2, CH_4 and N_2O (Zaman et al., 2021), and stimulating C fixation and storage in the soil (Begum et al., 2019; Santoyo et al., 2021; Zhu et al., 2022b). Conversely, soil microbe diversity, abundance and activity are dependent on climate changes, resulting in an interdependent relationship (Guo et al., 2020; Yuan et al., 2021; Tiedje et al., 2022). Climate change, that is increasingly intensified by human activities, can impact soil microbial community structure (Yu et al., 2018; Deltedesco et al., 2020; Zhou et al., 2020; Guerra et al., 2021; Mukhtar et al., 2021). Soil microbial functioning is affected by climate change because of changes to the biomass and community structure, while alterations in soil pH affect the diversity of soil microorganisms (Zhou et al., 2020).

Soil fauna is another important driver for C processing by microbiota. Macrofauna has a role in C turnover through direct metabolism, material fragmentation, organic carbon redistribution in the soil, and influencing microbial processing (Guidi et al., 2022). Considering the organic matter processing, the gut microbiome of fauna can accelerate the processing of recalcitrant organic material through the soil-dwelling humivorous fauna (Lou et al., 2022). The effects of soil fauna also were detected in greenhouse gases emission (Li et al., 2023).

FACTORS AFFECTING SOIL MICROBIAL ACTIVITY AND ORGANIC CARBON PROCESSING

Fluxes of C to and from soil depend on various environmental factors that influence C fixation by plants, organic matter deposition, and chemoorganotrophic microorganism activity in the soil. The main factors contributing to microbial activity are temperature, water, pH, nutrient availability, redox potential and organic substrate quality (Silva-Sánchez et al., 2019; Raza et al., 2023).

Temperature and moisture are two key factors that affect the synthesis, decomposition, and mineralization of organic matter. Temperature, as an energy form, directly affects biochemical reactions, meaning that most microorganisms (psychrophiles, mesophiles, and thermophiles) experience greater metabolism from about 0 °C to a plateau at approximately 25–39 °C and a decline to a minimum at about 65 °C. Even though water is necessary for life as a solvent in biochemical processes, it nevertheless affects how nutrients diffuse and predominate, and which molecules serve as the cell's final acceptors during respiration, which ultimately affects redox potential (Husson, 2013; Marschner, 2021).

Soil pH tend to be measured and represented as a variable in 'macroscopic' soil samples; however, in the heterogeneity of the soil, microhabitats with different pHs occur. In the microhabitats, pH drives nutrient solubility and biochemical activities, which influence carbon processing (Malik et al., 2018). In addition, nutrient availability also affects microbial activity and carbon flux. Nutrient availability is determined by the pH, mineralogy, concentration of surface charge, weathering level, quality and rate of organic matter processing. Thus, there is an interdependence between nutrient availability and organic matter dynamics (synthesis by plants and processing by microbiota).

Redox potential is a driver of metabolism. Actually, it indicates the environment condition promoted by the fluxes of electron acceptors and the past microbial activity. In a status of slow diffusion of O_2, this electron acceptor is consumed, a series of anaerobic metabolisms are imposed, and the diffusion of other electron acceptors continues. Jointly, there is a reduction in the C processing in each lower level of redox potential. Those aspects in soil are described below for anaerobioses conditions.

Various attributes of organic substrates, such as nutrient, cellulose, and lignin concentrations and the ratio between C and nutrient content, influence C mineralization by microorganisms and storage in the soil (Coonan et al., 2020; Liu et al., 2022). Microorganisms that metabolize organic substrates need mineral nutrients for cell maintenance and multiplication. The nutrients required in larger quantities by microbial growth in response to a supply of organic matter are N, P and S (Khan et al., 2016; Z. Zhu et al., 2022b). Substrates with C:N, C:P and C:S ratios below 20, 200, and 200, respectively, are considered rich substrates because they provide sufficient nutrients for microbial activity, resulting in a positive balance of nutrients in the soil. Conversely, poor substrates, with C:N, C:P and C:S ratios greater than 30, 300, and 300, respectively, require nutrient uptake from the soil for metabolization, resulting in a positive balance of mineral nutrient immobilization by soil chemoorganotrophic microorganisms and temporary reduction in nutrient availability in the soil (Kamble and Bååth, 2014; Ntonta et al., 2022). Thus, organic C metabolization is slower in poor substrates such as straw grass, resulting in organic material that remains on the soil surface for longer periods. The inverse occurs when legume straw or mineral nutrients are deposited in the soil. Greater nutrient content leads to faster organic carbon mineralization (Kamble and Bååth, 2014; Nottingham et al., 2018; Ntonta et al., 2022).

In addition to impeding metabolization by microbes and subsequent C mineralization, greater concentrations of recalcitrant polymers and molecules, such as lignin and phenolic compounds, might enrich the organic matter of the soil. Deposition of recalcitrant organic material in the form of coniferous needles and branches contributes to organic matter accumulation in soils (Hågvar, 2016; Růžek et al., 2021). Thus, these conditions, found in areas with long winters and sufficient rain to sustain the coniferous forests, play a significant role in the sequestration and storage of C in the soil (Gavrikov et al., 2016; Lugato et al., 2021). It is worth noting that this pattern can also be observed in a humid subtropical climate with regular rainfall, well-defined seasons, where temperatures can reach 30 °C in summer, but with the possibility of temperatures below zero in winter (Dieleman et al., 2013). This can occur under Araucaria forests in South America, for example (Dieleman et al., 2013; Gomes et al., 2023).

Water, temperature, pH, redox potential, organic matter quality are factors greatly regulated in the soil by the climate, topography, soil texture, mineralogy, and land-use, and thereby control natural influxes and effluxes of soil carbon (Lamichhane et al., 2019; Yun et al., 2019). Thus, these aspects are discussed below.

ENVIRONMENTAL REGULATORS FOR MICROORGANISMS AND C FLUXES IN THE SOIL

Climate

Temperate or colder and humid climates favor the growth of forest-like vegetation, such as coniferous forests, which promotes C sequestration through photosynthesis and deposition of relatively abundant organic matter on the soil surface (Figure 2) (Wiesmeier et al., 2013; Scharlemann et al., 2014; Hüblová and Frouz, 2021). Coniferous needles have higher levels of lignin and phenolic compounds that accumulate through deposition and decomposition (Hågvar, 2016; Růžek et al., 2021). At the same time, the

lower temperatures of the boreal climate reduce catabolic activity in the soil relative to tropical and equatorial climates (Chen et al., 2020; Lugato et al., 2021; Sokol et al., 2022b). As a result of recalcitrant organic matter deposition and reduced mineralization, soils in cold humid climates can hold significantly greater quantities of organic carbon. This organic carbon accumulation is well exemplified in boreal forest (taiga) soils (Pan et al., 2011; Gavrikov et al., 2016; Lugato et al., 2021).

Warm and humid climates with high levels of precipitation, such as those found in equatorial and humid tropical areas, propitiate rainforests, and can contribute to the accumulation of organic matter in the soil (Blais et al., 2005; Pan et al., 2011). Higher temperatures and soil moisture, with relatively rapid microbial mineralization of soil organic material, support forest growth and high photosynthetic capacity, which in turn lead to substantial fluxes of C from the atmosphere to organic molecules in the vegetation and finally to the soil (Figure 2). Thus, tropical rainforests have relatively high levels of organic matter in the soil (Pan et al., 2011; Sokol et al., 2022b), despite and because of the faster turnover of C, which leads to nutrient mineralization that is sufficient to sustain rapid plant growth (Vitousek and Sanford Jr, 1986; Paula et al., 2021).

Higher soil moisture tends to stimulate C accumulation by reducing the rate of organic matter mineralization (Figure 2). Soils with sufficient organic matter and water saturation due to deficient drainage undergo O_2 depletion (Marschner, 2021). The consumption of O_2 is prompted by aerobic populations that use organic molecules as reduced substrates that provide C and energy. In aerobic metabolism, the substrate is oxidized, and the final electron acceptor is reduced, transforming O_2 into H_2O. When the soil is saturated with water, i.e., when pores are filled with soil solution, O_2 diffusion is insufficient to support activity among aerobic populations (Husson, 2013; Marschner, 2021). Oxygen depletion and competition for resources favor microbial populations that can use/respire other electron acceptors to produce energy (Marschner, 2021). Successional anaerobic communities use the main electron acceptors in the descending order of predominance and potential for energy use: NO_3^-, Mn^{4+}, Fe^{3+}, SO_4^{2-} and CO_2 (Figure 3). Thus, redox potential is gradually reduced through the succession of anaerobic metabolism if there is sufficient organic substrate to maintain biological activity. At the lowest level of redox potential, CO_2 can be used by methanogenic populations, resulting in CH_4 gas emissions. It is worth noting
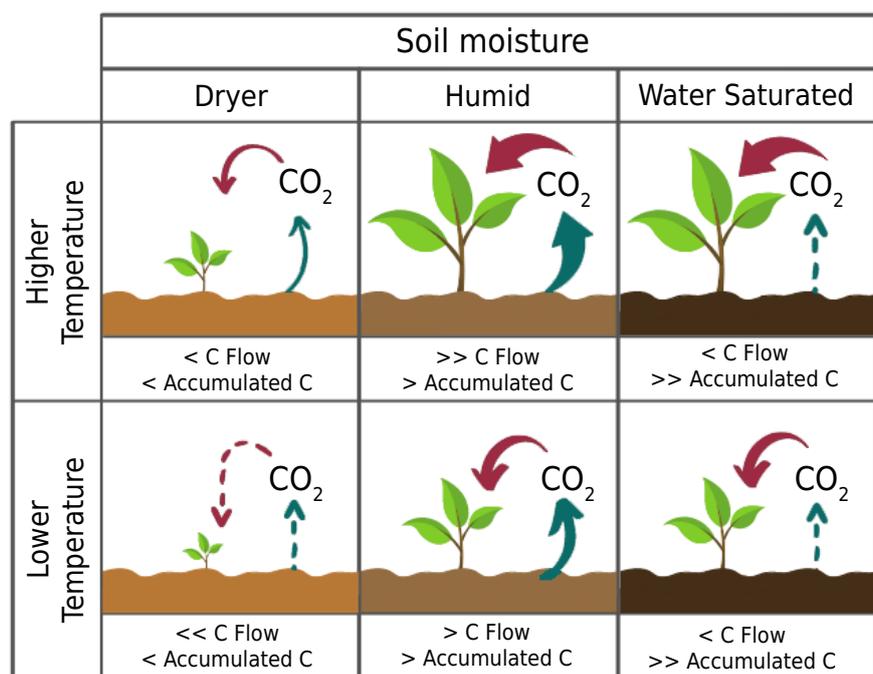

Figure 2. Effect of temperature and soil moisture on natural influxes and effluxes of C to and from the soil and their influence on plant growth and mineralization of C by soil microorganisms.

that, in addition to CH_4, anaerobic conditions also promote NO_3^- respiration and emissions of another potent greenhouse gas - N_2O (Marschner, 2021). The reduced energy yield from anaerobic metabolism results in slower organic matter decomposition and microbial growth (Ponnamperuma, 1972; Marschner, 2021), allowing the accumulation of organic carbon in waterlogged soils.

Conversely, arid climates tend to present lower C fixation and emissions from soil, especially in colder climates (Lal, 2009). Even in warm but dry climates, such as those in tropical dry forests in Caatinga Biome and other worldwide semi-arid regions, occur lower C fixation by photosynthesis and organic matter processing by the soil microbiota due to the lower soil moisture (Menezes et al., 2012; Santos et al., 2019).

In general, considering the balance of C that is contributed by plant material deposition and the C lost from organic matter mineralization by chemoorganotrophs, organic carbon is mostly stocked in soils under cool humid and tropical/equatorial humid climates, or when soils are saturated with water and plant growth supplies sufficient organic matter (Figure 2).

Climate change can affect the structure and activity of soil biological communities. Confirmatory data from IPCC Sixth Assessment Report on climate change has become increasingly robust (Masson-Delmotte et al., 2021; https://www.ipcc.ch/assessment-report/ar6/). Studies have shown that CO_2–rich environments lead to greater C fixation by plants (Niklaus et al., 2001; Dusenge et al., 2019). An environment with a CO_2-rich atmosphere implies a better supply of carbon for photosynthesis, which could increase fixation and promotes plant development (Kuzyakov et al., 2019). These conditions should increase root exudation and organic substrate availability in the rhizosphere, increasing CO_2 emissions due to the faster processing of organic matter. In addition to the increase in root exudation rates, there are indicative that warming alters exudates and soil organic matter composition (Xiong et al., 2019). Therefore, climate change also affects soil biota and its processes, including the primary production of organic matter, its further degradation, and C mineralization (Yu et al., 2018; Zhou et al., 2020; Guerra et al., 2021). However, the ways that plant and microorganism growth may impact soil nutrient mineralization and uptake, and the dynamics of soil organic carbon content are poorly understood and challenging to discover (Kuzyakov et al., 2019; Terrer et al., 2021). Thus, further studies should be made to understand the rate of matter and energy cycling and the effects on soil organic carbon stocks in a warmer and CO_2–rich atmosphere.

Metabolism	Final acceptor and reduced product of respiration	Potential		
		Cell energy production	Mineralization of organic carbon	Soil carbon accumulation
Aerobic	$O_2 \rightarrow H_2O$			
Anaerobic	$NO_3^- \rightarrow N_2O, N_2$			
	$MnO_2 \rightarrow Mn^{2+}$			
	$Fe^{3+} \rightarrow Fe^{2+}$			
	$SO_4^{2-} \rightarrow H_2S$			
	$CO_2 \rightarrow CH_4$			

Figure 3. Successional metabolism according to the electron final acceptors in cell respiration and the respective potential for microbial mineralization of organic carbon in situations of low O_2 diffusion and sufficient quantities of organic carbon.

Climate change also increases the frequency of extreme weather events. Severe drought reduces soil moisture (Grillakis, 2019; Li et al., 2020), hindering biological activity, including organic matter mineralization and nutrient release. Atypical droughts also affect plant productivity (Li et al., 2020) and the subsequent deposition of organic carbon to the soil. In addition, stronger precipitation events can erode soil (Pal et al., 2021; Panagos et al., 2021), move large masses of soil with landslides (Li et al., 2022), and cause floods (Mullan et al., 2019). Events like these can move significant volumes of particles and organic matter (Gervais-Beaulac, 2013), resulting in new soil formation, modified plant production, and consequent changes in carbon flux. In addition, saturated soils in flooded areas increase anaerobic metabolism, which can lead to methanogenesis and CH_4 emissions (Sánchez-Rodríguez et al., 2019).

Topography

The lowest areas of relatively flat lowlands, with sufficient precipitation, tend to have higher moisture, greater nutrient levels, and consequently higher plant productivity than in higher areas, contributing to a greater supply of organic C to the soil (Figure 4) (Pei et al., 2010; Zhao et al., 2014; Likhanova et al., 2022). Groundwater pools in the lowest parts of this landscape, which may lead to saturation and flooding (Crave and Gascuel-Odoux, 1997; Thompson et al., 1997). Soils rich in organic matter, such as Histosols, can develop in those areas with low or no water movement and sufficient organic matter (Kolka et al., 2016).

Low-lying areas can also accumulate soil and sediment particles that have been transported by gravity and contain organic matter (Yoo et al., 2005; Kirkels et al., 2014) (Figure 4). Thus, some of the organic carbon fixed by photosynthesis in higher terrain can eventually accumulate at lower levels and increase the amount of organic matter in lowlands. Nevertheless, different landscapes can affect SOC concentration in different ways, which ultimately can be determined more by soil properties and plant growth than by topography (Tian et al., 2020).
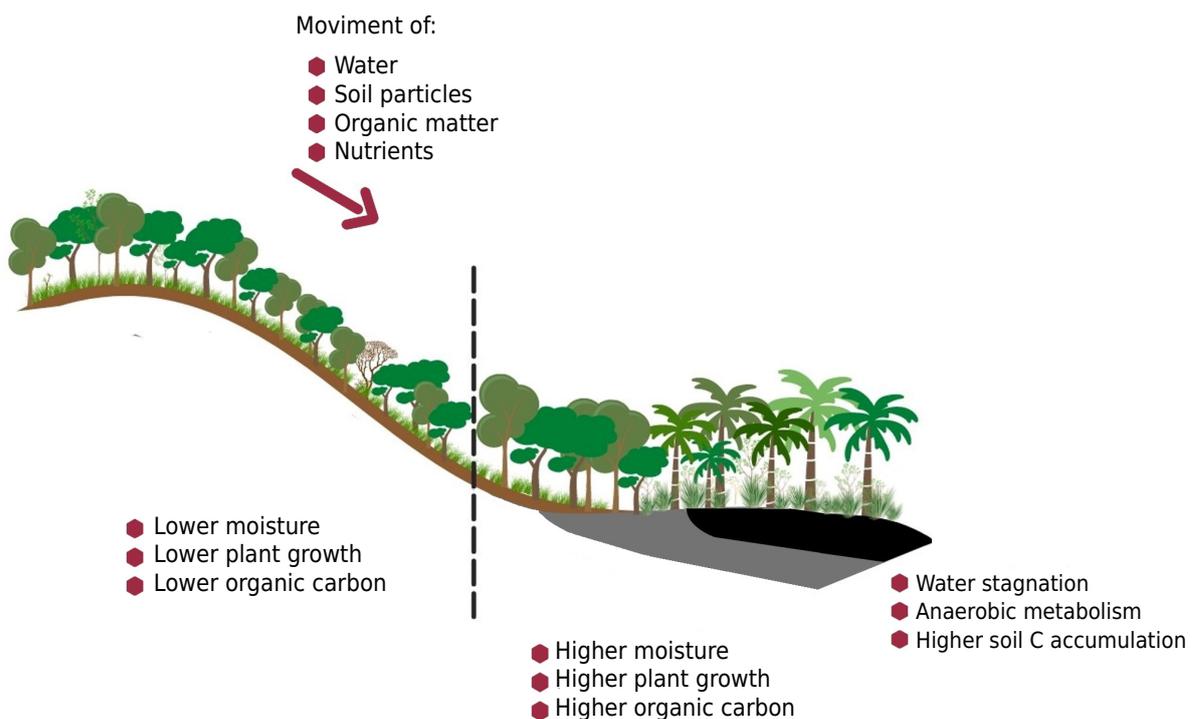

Figure 4. Influence of relief on soil moisture, plant growth, and organic carbon flow in climates without severe dry seasons.

Soil texture and mineralogy

Although soil solid phase is made up of organic and mineral particles, most soils are predominately composed of mineral material. Of the three particle sizes – sand, silt and clay – the smallest has the most significant impact on surface interactions. Thus, clay content favors larger and more occluded microaggregates and is positively correlated with SOC (Oades, 1988; Schweizer et al., 2019; Matus, 2021; Oliveira et al., 2023) because of lower biodegradation rates. Organic matter can be occluded within and protected from microbial and enzyme attacks by clay, which contributes to soil microaggregates (Oades, 1988; Sposito et al., 1999; Keiluweit et al., 2018). Additionally, clayey soils tend to have more micropores and lower O_2 diffusion than coarser soils, which inhibits the oxidation of organic C by aerobic metabolism (Keiluweit et al., 2018). Mineralogy can also affect outflows of soil C. Less weatherized clay minerals such as expansible 2:1 clay (e.g., smectites and vermiculites) present relatively higher specific surfaces. In addition, secondary sesquioxides and allophane can strongly bind with organic matter by forming inner-sphere organo-mineral complexes (Singh et al., 2017). This greater area of interaction provides stronger links between minerals and organic matter (Sposito et al., 1999; Singh et al., 2017). Thus, higher content of these minerals contributes to soil aggregation and organic carbon occlusion and thereby hindering O_2 diffusion and organic matter metabolization.

Land-use

Most changes in land-use involve transforming native areas into agricultural lands (Ellis, 2021). This process can reduce soil organic carbon in two main ways. First, influxes of organic matter are reduced by replacing natural vegetation with crops that are harvested and not left to enter the soil (Powlson et al., 2022). Second, SOC content is reduced by tilling the soil, which stimulates aerobic chemoorganotrophy and C efflux from the soil through CO_2.

Effect of no-tillage systems on CO_2, CH_4 and N_2O emissions seems to depend on climatic conditions. Meta-analysis of data from no-tillage systems in temperate or sub-tropical climates showed increases in greenhouse emissions (Shakoor et al., 2021, 2022) while in tropical humid climates, no-tillage reduced CO_2 and other greenhouse gas emissions (Passianoto et al., 2003; La Scala Jr et al., 2006; Ramborun et al., 2021) and increased SOC (Ogle et al., 2019).

Aiming to conserve soil and counterbalance climate change, a set of practices that have been adopted is climate-smart agriculture (CSA) (Oliveira et al., 2023). The CSA mainly involves no-tillage, organic amendments, cover cropping, crop-livestock, livestock-forestry, and crop-livestock-forestry. In a review study of these practices in the Cerrado Biome in Brazil, where the predominant climate is Aw (Köppen classification system) and savanna phytophysiognomies occur, there are indications of an increase in SOC with the adoption of CSA (Oliveira et al., 2023). Compared to afforestation and pasture, the highest SOC stocks were found under CSA (131 Mg ha^{-1}), being similar to those under native vegetation (129 Mg ha^{-1}) when considering the 0.00-1.00 m layer. Among CSA management systems, no-tillage (1.24 Mg ha^{-1} yr^{-1}) and crop-livestock-forestry (1.47 Mg ha^{-1} yr^{-1}) are those with a higher increment of SOC in the 0.00-1.00 m layer. The study generally points out the CSA as a strategy to increase SOC stocks in agricultural areas in the Cerrado Biome and contribute to counterbalancing anthropogenic C emissions (Oliveira et al., 2023).

Overall, conservative practices such as crop rotation, cover crops (Solanki et al., 2019; Wiesmeier et al., 2019; Cordeiro et al., 2022; Jordon et al., 2022), organic amendments, organic farming (Han et al., 2017) and no-tillage (Liu et al., 2021; Ramborun et al., 2021) reduce losses and or promote the entry of organic carbon into the soil (Figure 5). Forest and grassland ecosystems are not subject to soil turnover and can contribute to C flux and storage in the soil via shoot, leaf and root deposition (Ogle et al., 2019; Panchal et al., 2022).
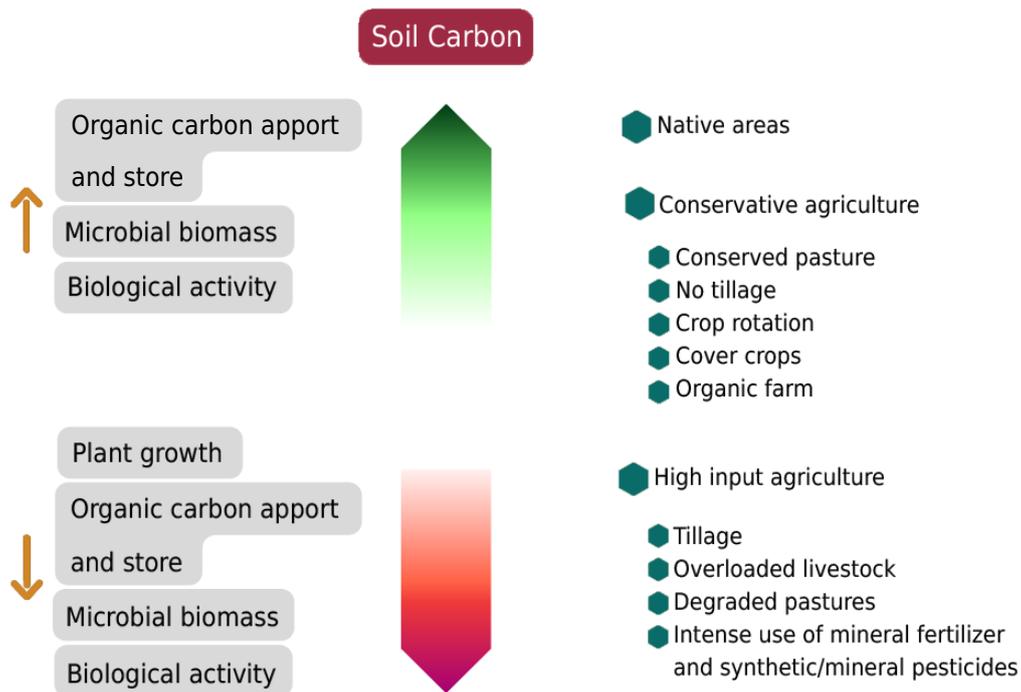
Soil Carbon

Organic carbon apport and store

Microbial biomass

Biological activity

Native areas

Conservative agriculture

Conserved pasture
No tillage
Crop rotation
Cover crops
Organic farm

Plant growth

Organic carbon apport and store

Microbial biomass

Biological activity

High input agriculture

Tillage
Overloaded livestock
Degraded pastures
Intense use of mineral fertilizer and synthetic/mineral pesticides

Figure 5. Soil organic carbon varies by land-use, occupation, and management within an ecosystem or biome.

Deposition of microbial nutrients has been shown to have effects on SOC. Excess N deposition in soils under tropical forests increased C stocks and suggests that those soils can function as a sink of C and elevated N generated by human activities (Lu et al., 2021). However, in an 11-year assay with dried corn leaves and roots, N and P addition selectively modified the microbial carbon decomposition: N increased litter decomposition, while P prevented the decomposition of soil carbon (Zhang et al., 2022). Furthermore, N and P addition in six grasslands on different continents did not influence microbial carbon use efficiency and biomass turnover time, suggesting that despite significant changes in element inputs, microbial carbon use did not vary much (Widdig et al., 2020). Therefore, more investigation should be done to shed light on the effects of nutrient deposition on SOC stocks.

Soil compaction by cattle and machinery decreases pore space and O_2 diffusion and leads to anaerobic metabolism in the microhabitats of the compacted layer (Berisso et al., 2012; Longepierre et al., 2021). Thus, in the presence of organic substrates, successive consumption of final electron acceptors occurs until CO_2 is used by methanogenic populations, resulting in CH_4 gas emissions (Husson, 2013; Yadav et al., 2020). Conversely, the lower porosity of some compacted peat soils can reduce CH_4 emissions (Busman et al., 2021).

Intensive and non-conservative use of the soil can also lead to land degradation. The organic matter concentration and carbon fixation potential of these soils are typically lower. There is an estimated 1 to 6 billion hectares of degraded land worldwide (Gibbs and Salmon 2015). Thus, land reclamation is a practical strategy for reclaiming environmental soil functions, such as water infiltration and quality (Issaka and Ashraf, 2017; Lilburne et al., 2020; Steinhoff-Knopp et al., 2021), carbon fixation, and storage (Siqueira et al., 2020; Lal et al., 2021), and improving consequent economic benefits (Nkonya et al., 2016). Some soil microorganisms can aid land restoration by promoting plant growth. Plant growth-promoting microorganisms can be applied as inoculants or stimulated by management practices. For example, selecting and growing plant species with N-fixing associates can stimulate C input into the soil under reforestation and forest management practices (Mayer et al., 2020).

In summary, conservative practices, such as no-tillage, regenerative and organic agriculture, increasing plant diversity, and crops with dense root system species can contribute to the increase and stock of carbon in the soil. The effects of nutrient additions on soil carbon accumulation still need further studies for confirmation.

METHODS FOR QUANTIFYING CARBON EMISSIONS FROM SOIL

There are direct and indirect methods for measuring the microbial processing of organic matter and carbon emissions. Gases emitted from the soil can be collected directly from the field, for example, with a chamber hood (Brummell and Siciliano, 2011; Popin et al., 2020; Quiñones et al., 2022) or portable devices (Panosso et al., 2009). There is also the possibility of using C isotopes (^{13}C, ^{14}C) to understand the dynamics and emission of C in the soil in the form of CO_2 and CH_4 (Estop-Aragonés et al., 2020; Xu et al., 2023; Liu et al., 2024).

Soil incubation assays, such as soil basal respirometry, are used for measuring carbon loss. That *in vitro* microcosm assay evaluates CO_2 emission with NaOH and titration with HCl (Alef, 1995). Since the physical conditions are different from those in the field, it represents a potential for processing and mineralization of soil organic matter. Coupled with this method, the microbial biomass C determination (Vance et al., 1987; Wu et al., 1990) is essential to determining the mineralization capacity of organic matter per mass of microorganisms. The ratio of C-emitted:C-microbial biomass is the metabolic quotient (Anderson and Domsch, 1993), which indicates the community energy efficiency for cell maintenance and multiplication. The higher metabolic quotient values indicate community stress since the CO_2 emitted per biomass is higher.

Some methods measure biochemical potential and not necessarily the metabolical processing of organic matter in the field. Enzymatic activities, identification of enzymes by proteome, or their transcribed genes by transcriptome support understanding the soil organic C dynamics (Zhang et al., 2021; Panettieri et al., 2022). However, these methods indicate the potential for metabolizing organic matter and not necessarily the emission of CO_2 and CH_4.

The methods generally do not differentiate whether the origin of CO_2 and CH_4 is from microorganisms or other soil organisms. One way to measure the emission of C from the soil by organisms is by the decrease in organic material. The litterbag method consists of placing prepared organic material inside a bag with a determined mesh size (Faust et al., 2019; Chassain et al., 2021). This allows you to select the size of the soil organism that will have access to the organic substrate. The reduction in the mass of material within the litterbag indicates the soil's potential to mineralize organic matter. In this sense, it is necessary to consider that soluble organic molecules can leave the litterbag through leaching in rainy seasons.

SOIL MICROORGANISMS TO COUNTERBALANCE C EMISSION – ROLES TO C INFLUX AND STORAGE IN THE SOIL

Plant growth-promoting microorganisms

Some microbial isolates, called plant growth-promoting microorganisms (PGPMs), can colonize the rhizosphere, plant surfaces, or inner tissues and establish potentially mutual relationships that increase plant growth while providing a carbon and energy source to the microbial partner (Adeleke and Babalola, 2021; Hakim et al., 2021). Some rhizobacteria can fix atmospheric N, solubilize nutrients, synthesize or influence plant growth regulators, or control root pathogens (Shameer and Prasad, 2018; Brunetti et al., 2021; Zeng et al., 2022).

Plant growth-promoting fungi can contribute to nutrient mineralization and solubilization, phytohormone synthesis, pest control, and stimulation of plant defenses (Lin et al., 2021; Poveda et al., 2021; Mohamed et al., 2022). Different mechanisms bring about nutritional improvement. For example, entomopathogenic fungi can establish associations that transfer N and C from infected insects to plants (Behie and Bidochka, 2014; Behie et al., 2017). Application of some fungal isolates promotes plant growth (Alves et al., 2021; Barbosa et al., 2022) and soil improvement, as *Purpureocillium lilacinum* increased organic carbon in the soil under common bean (Alves et al., 2021). Mycorrhizal fungi have an intimate relationship with their plant hosts that was wrought by joint evolution and which contributes to plant uptake of P, N and other nutrients. The section below about Mycorhiza provides a deeper look at the roles that root-fungi symbioses play in C flow.

Overall, PGPM may benefit C fixation by plants and may contribute to organic matter input into the soil (Figure 6). Consortia of multiple PGPM can afford a minimum of functional diversity that ensure these positive effects under a variety of environmental conditions (Santoyo et al., 2021). Thus, finding and applying efficient microbial isolates adapted to each plant-soil-climate is crucial for developing technological practices that target higher C sequestration.

Mycorrhiza

Mycorrhizae encompass mutual symbiosis between some soil fungi and roots, which includes the growth of hyphae inside the roots and the spread of mycelium through the soil (Smith and Read, 2008). This association contributes to increasing the volume of soil utilized and generally improves nutrient uptake (mainly P) and water uptake. In return, plant hosts provide carbohydrates and lipids to mycorrhizal fungi. Hyphae also participate in soil aggregation, mainly by enmeshing particles (Morris et al., 2019). As a result, mycorrhiza contributes to plant growth, soil structure and porosity, water infiltration, and resistance to hydric erosion.

Up to 85 % of superior plant families form mycorrhiza, which are virtually present in all vegetated soil (Smith and Read, 2008; Brundrett and Tedersoo, 2018). The most common types of symbiosis are ectomycorrhiza (EcM) and arbuscular mycorrhiza (AM).
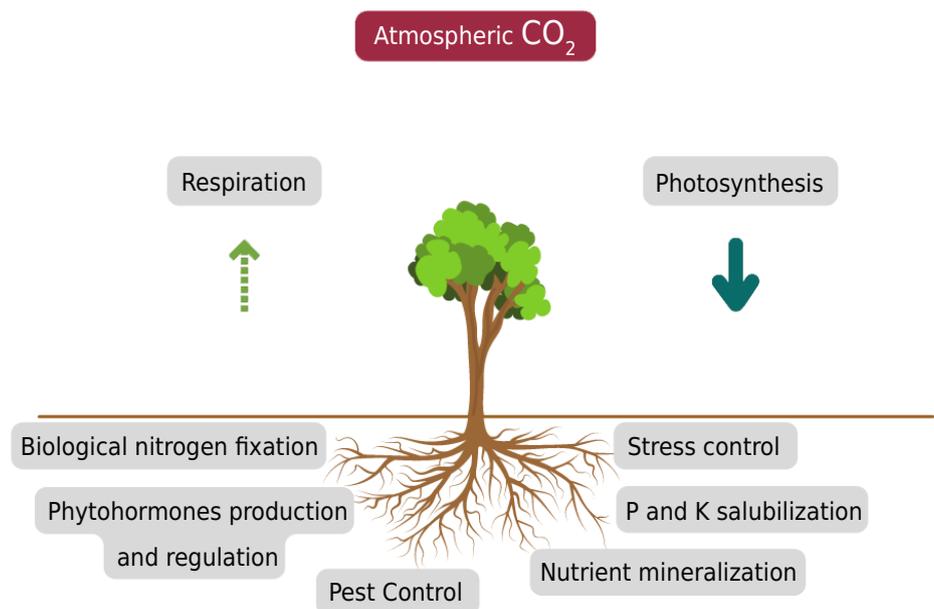

Figure 6. Effects of plant growth promoting microorganisms on organic carbon stock in the soil.

Ectomycorrhiza involves some basidiomycetous and ascomycetous fungi predominantly associated with tree species in temperate climates (Smith and Read, 2008; Peay et al., 2016). Arbuscular mycorrhiza fungi (AMF - Glomeromycota) form associations with most plant species that have roots (80 %) (Smith and Read, 2008; Brundrett and Tedersoo, 2018), being the most common mycorrhiza in tropical plant communities but is also commonly found in other climates. The AM symbiosis also forms in most crop and forage species.

Given their impact on plant growth (Begum et al., 2019; Wen et al., 2022), mycorrhiza can play a significant role in C flow through fixation and organic matter deposition on the soil (Figure 7). Knowledge of the contribution of mycorrhizae to soil C input is not yet well established. However, there are estimates of the C values allocated by mycorrhizae in the soil. The hyphae, fungal fruiting body, spores, and exudates constitute temporary storage of organic C (Ren et al., 2021; Zhu et al., 2022a). Nevertheless, few studies discriminate the C pool between these fungal structures, indicating instead the total mycelium and exudates C in the soil. Per year, there is an estimated allocation of 3.58 Gt of C fixed in photosynthesis to mycorrhizal fungi in the soil, with 1.07 Gt C to arbuscular mycorrhiza, 2.47 Gt C to ectomycorrhizal fungi, and 0.03 Gt C to ericoid mycorrhizal fungi (Hawkins et al., 2023). Part of this C is temporarily stocked in soil, as (1) it is used for mycelial build and maintenance, (2) remains as fungal necromass in the soil, and (3) is released as exudates. On the other hand, part of the allocated carbon to mycorrhiza is emitted into the atmosphere as the organic substrate is consumed in respiration.

Glomalin-related soil proteins (GRSPs) are mostly indicated as a gene product from AMFs but also encompass other organic molecules (Irving et al., 2021). The GRSPs generally correlate positively with AMFs, SOC and aggregate stability (Agnihotri et al., 2022). It can be more recalcitrant than other soil organic material, thus accumulating in the soil through time and acting as an important compartment of C stock (Rillig et al., 2001; Irving et al., 2021). In a chronosequence of soil classes, glomalin contributed 1.25 to 5.1 % of the total C in the O and A horizons (Rillig et al., 2001).

Mycorrhizal hyphae also contribute to C fluxes by enmeshing particles, which promotes soil aggregation (Morris et al., 2019; Jeewani et al., 2021) and provides some stability to the organic matter within the aggregates that can resist microbial degradation and emission of C-containing gases (see section below on *soil aggregation by soil microorganisms*).
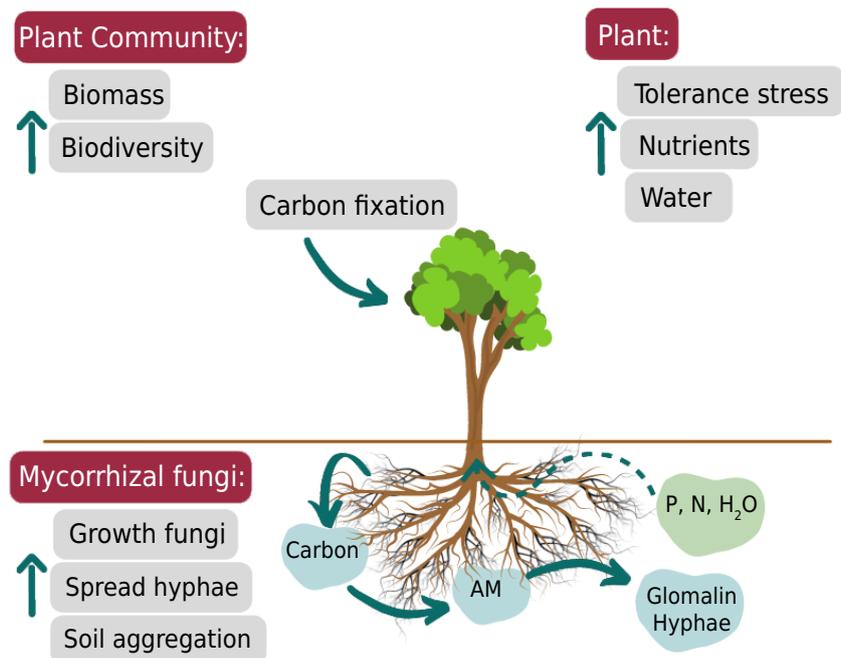

Figure 7. Effects of mycorrhiza on plant growth and organic carbon stock in the soil. AM: arbuscular mycorrhiza.

Ultimately, the balance of C influx in soil is positive since fungi return plant-derived carbon back to the atmosphere at rates of 1-6 % for AM, and 1-19 % for EcM (Hawkins et al., 2023). Therefore, practices for establishing effective fungal isolates adapted to specific conditions can help combat climate change by contributing to C sequestration and eventual deposition and storage in the soil.

The potential of each fungus varies considerably given the diversity of plants, even within a crop rotation program, and the amplitude of soil and climatic conditions. In other words, a mycorrhiza fungus isolate may significantly contribute to plant growth in a given soil-plant-climate circumstance, but may not be effective in other scenarios (Dodd and Thomson, 1994; Cruz-Paredes et al., 2020). Therefore, applying a consortium of effective mycorrhizal fungal isolates increases the probability of stimulating plant growth (Crossay et al., 2019, 2020). Crop rotation, cover crops, and mycotrophic plants can also promote plant diversity and stimulate AMF communities (Brito et al., 2021). Mycorrhiza establishment is further aided by crop systems that employ fewer external inputs, particularly less phosphorous fertilizer, and fungicides and organic farming (Wahdan et al., 2021; Kuila and Ghosh, 2022). No-tillage is another conservative method that benefits arbuscular mycorrhiza since turning the soil disrupts the hyphae network (Kuila and Ghosh, 2022).

Therefore, the impact on plant growth is greatest when effective mycorrhizal fungi isolates are selected and when a consortium of isolates is applied (Crossay et al., 2019, 2020). In addition, the AMF community can be stimulated by increasing plant diversity through crop rotation, cover crops, and mycotrophic plants (Brito et al., 2021). Crop systems that need fewer external inputs, specifically P fertilizer and fungicides, and organic farming (Wahdan et al., 2021; Kuila and Ghosh, 2022) also contribute to mycorrhiza establishment. Since turning the soil disrupts the hyphae network, no-tillage is another conservative practice that benefits arbuscular mycorrhiza (Kuila and Ghosh, 2022).

Soil aggregation by soil microorganisms

Soil aggregation contributes to protecting organic C against microbial mineralization by shielding organic material within the aggregates, which prevents soil microbes and abiotic enzymes from accessing the molecules (Figure 8) (Oades, 1988; Sposito et al., 1999;
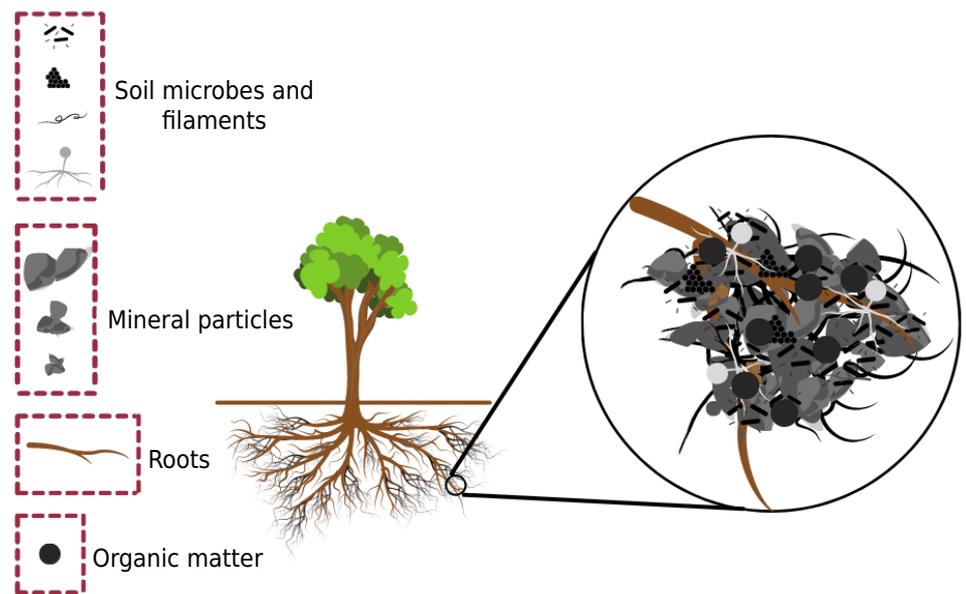

Figure 8. Soil aggregation contribution on protecting organic matter from enzymatic degradation.

Keiluweit et al., 2018). Additionally, even though soil aggregation creates both macro and microporosity, in some microhabitats, O_2 diffusion may be limited in micropores, thereby reducing the aerobic mineralization of organic materials (Keiluweit et al., 2018).

Soil aggregation is achieved by physical and chemical processes in association with soil biological activity (Pereira et al., 2021). Soil microorganisms also play a significant role in the arrangement of soil particles, mostly through filamentous fungi that enmesh particles, but also by cementing compounds generated by soil microorganisms (Costa et al., 2018; Morris et al., 2019; Rabbi et al., 2020; Pereira et al., 2021). Therefore, some soil microorganisms promote C storage by accumulating biological structures such as hyphae and polymers, which in turn participate in soil aggregation and provide protection against the mineralization of organic matter.

SOIL MICROORGANISMS THAT ENABLE C EFFLUX FROM THE SOIL

Organic C mineralization by soil microorganisms

Organic molecules can incorporate energy captured from electromagnetic radiation via photosynthesis. This is the primary way that CO_2 is captured from atmosphere and eventually incorporated into the soil. Most soil microorganisms are chemoorganotrophs that use reduced organic substrates as electrons source for obtaining energy and C for multiplication (Plante et al., 2015). Furthermore, the use and oxidation of C molecules by soil cells give rise not only to other organic molecules and by-products, but also to the mineralization of C in the form of CO_2 gas, which returns to the atmosphere (Figure 1).

Given the great biodiversity in the soil, and limitations on resources for microbial activity, an increase in one factor, such as organic C or mineral nutrient supply, accelerates metabolization and C outflow as CO_2 via soil respiration (Wang et al., 2019; Liang et al., 2022). In addition, changing land-use from native to agricultural soils promotes the mineralization of organic C through aeration caused by turning the soil that ruptures aggregates (Six et al., 1999; Silva et al., 2022; Powlson et al., 2022). Thus, more conservative land-use practices can limit CO_2 emissions and promote net gains of C accumulated in the soil (Liu et al., 2021).

Effect of the rhizosphere on C efflux

Rhizosphere is the portion of the soil affected by the presence and roots activity. It contains more numerous and active microorganisms than in bulk soil (Ling et al., 2022; Zhao et al., 2022). Organic molecules deposited around the roots drive this activity. Therefore, C flows from atmospheric CO_2 to plants via photosynthesis. Part of this C is then released into the soil through root exudation, epidermic cell lysis (caused by soil fauna grazing, friction against particles or emergence of secondary roots), and exudation from mycorrhizal fungi (creating the mycorrhizosphere). These organic molecules provide a substrate that is eventually mineralized to CO_2 by soil microorganisms (Zhao et al., 2022). On the other hand, rhizodeposition also supplies stabilized C by storing C in the soil (Sokol et al., 2019; Panchal et al., 2022). Therefore, the rhizosphere positively affects SOC processing by providing higher levels of SOC, microbial biomass C and CO_2 emissions than bulk soils (Zhao et al., 2022).

Methanogenesis in the soil

Methanogenesis is a process of anaerobic metabolism that occurs in environments with extremely low redox potential (Husson, 2013; Marschner, 2021). Low redox potential is created by the consumption or absence of a final electron acceptor with a higher capacity to produce energy than CO_2. Thus, in the presence of organic molecules and

low O_2 diffusion, communities deplete final electron acceptors successively, from NO_3^-, Fe, Mn, to SO_4^{-2}, until reaching methanogenesis and using CO_2 for respiration (Figure 3). Methanogenesis can occur in the digestive system of vertebrate and invertebrate animals (Horváthová et al., 2021; Misiukiewicz et al., 2021; Mizrahi et al., 2021) or in environments with stagnant water, relatively low or no O_2 diffusion, and sufficient levels of organic carbon as a substrate to sustain methanogenic activity (Husson, 2013; Gao et al., 2019; Marschner, 2021). It is worth noting that methane can also be produced in the presence of oxygen, likely by all living cells, in response to oxidative stress inducers (Ernst et al., 2022).

Methanogenesis also exists in soils and may represent an important outflow of C. Wetlands, especially those formed by organic and peat soils, contribute significantly to CH_4 emissions (Gao et al., 2019; Jackson et al., 2020). Organic soils may contain approximately 550 Pg of C (Joosten and Couwenberg, 2008). However, drainage of organic soils significantly increases C efflux from soil because of aerobic mineralization of organic matter (Conchedda and Tubiello, 2020).

Considering climate change, special attention must be given to permafrost soils. Because of low temperatures and, consequently, lower biological activity, these soils can accumulate and store organic carbon. Estimates of the total organic C stocked in permafrost soils range from 530 to 1000 Pg (Hugelius et al., 2014, 2020). Warming and thawing of this formerly frozen layer promotes microbial activity and leads to two sources of carbon emissions: CO_2 from aerobic metabolism and CH_4 in water-logged anaerobic conditions (AminiTabrizi et al., 2020; Lu et al., 2022). One way to reduce CH_4 emissions from thawing permafrost would be to select and apply methane oxidizing isolates that act as bio-filters of methane production (Dang et al., 2022). Roadway development can contribute to permafrost warming; however, this thawing could be prevented by building air convection embankments (Goering, 2003).

Methane is even emitted from well-drained soils. Here, some microhabitats may have redox potential levels that are low enough to establish active methanogenic populations. The volume of microsites with low redox potential rises in areas of soil compaction or those with significant quantities of easily degradable organic molecules (Yadav et al., 2020; Longepierre et al., 2021). Even under conservative management practices, such as no-tillage or organic farming, straw and other organic material accumulation on the soil surface may increase CH_4 emissions (Shakoor et al., 2021). However, conservative land management practices can result in levels of organic matter and C storage sufficient to guarantee positive C flows into the soil (Liu et al., 2021; Ramborun et al., 2021).

SUMMARIZING APPROACHES TO USE SOIL MICROORGANISMS TO MITIGATE CARBON EMISSIONS

Additions, storage, and losses of soil carbon are mediated by soil microorganisms (Table 1). Some beneficial microorganisms contribute to soil inflow indirectly by stimulating plant growth. Soil organic carbon storage is promoted by soil aggregation, which physically protects organic matter against mineralization. Hyphae, living organisms, and metabolites contain organic molecules that temporarily store C in the soil. On the other hand, soil efflux is affected by microbial mineralization of the organic substrate when rhizosphere activity is pronounced. Methane is also emitted from the soil through methanogenic activity in both water-saturated and unsaturated soils. Thus, strategies can be developed to improve C influx and promote C storage in the soil, counterbalancing rising greenhouse gas emissions (Table 1).

Table 1. Proposed strategies to counterbalance increasing greenhouse gas emissions based on the main roles microorganisms play in global C flow

Flows to and from soil	Processes	Strategies to counterbalance C emissions to the atmosphere	References
Promoting C fixation	Plant growth-promoting microorganisms (PGPM)	• Selection and application of effective PGPM isolates and consortia in different soil-plant-climate conditions. • Reforestation or forest management, including species with N-fixing association.	Santoyo et al. (2021); Adeleke and Babalola (2021); Mayer et al. (2020)
	Mycorrhiza	• Application of effective mycorrhizal isolates and consortia in a range of environmental conditions. • Stimulation of AMF communities by: - Increasing plant diversity through crop rotation and cover crops. - Cultivating mycotrophic plants. - Avoiding or reducing the use of fungicides; Organic farming. - No-tillage crop systems.	Crossay et al. (2019, 2020); Brito et al. (2021); Wahdan et al. (2021); Kuila and Ghosh (2022)
Promoting C storage	Soil aggregation	• Increase soil organic matter through cover crops and organic amendment. • No-tillage. • Organic farming.	Ramborun et al. (2021); Liu et al. (2021)
C efflux	C mineralization in soil	• No-tillage. • Cover crops with more recalcitrant residues and higher C:N ratios such as grasses. • Cease draining organic soils in wetlands.	Liu et al. (2021); Liu et al. (2022); (Conchedda and Tubiello, 2020)
	Rhizosphere effect	• Stimulation of rhizosphere activity and organic matter deposition through crop rotation or consortium, including legumes and species with dense root systems such as grasses.	Solanki et al. (2019); Sokol et al. (2019); Panchal et al. (2022)
	Soil methanogenesis	• Conservative management of soils to avoid or reverse soil compaction. • Improvement of soil hydraulic conductivity. • Selection and application of methane-oxidizing isolates. • Modification of roadways to prevent thawing in permafrost areas.	Yadav et al. (2020); Berisso et al. (2012); Lu et al. (2022); Dang et al. (2022); Goering (2013)

CONCLUSIONS

Soil microorganisms represent a rich array of metabolic routes involved in C transformation. Among active microbiota, some participate in C efflux as CO_2 and CH_4 emissions, while others directly or indirectly promote C fixation, influx, and storage in the soil. Climate change affects the diversity and function of soil microbiota, which in turn impacts the biochemical processes that move C through the soil. One way to combat rising greenhouse gases in the atmosphere is to stimulate C fixation through photosynthesis. This could be achieved via soil microorganisms that promote plant growth and C storage. Thus, selecting, using, and stimulating beneficial microorganisms could replace part of the mined or synthetic inputs used to improve crop yields and ultimately help mitigate climate change. However, according to the multiplicity of possible effects in specific environmental conditions, studies are still needed to establish effective methods for promoting soil microorganisms aiming at the deceleration of greenhouse gas emissions. For example, the establishment and use of effective microbial isolates should be better investigated. In addition, the beneficial effects of N and P fertilization still need further studies for confirmation. It is noteworthy that the diagnosis of the SOC stock potential and strategies for increasing it must be planned for each soil and climate condition.

Moreover, no-tillage benefits to C storage appear to be dependent on soil features, such as organic carbon content, and local climate; thus, specific considerations must be done for each soil or farm production.

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